# ANALYSIS OF THE GENETIC COMPONENTS OF LIFE HISTORY PARAMETERS USING LABORATORY REARED *SIMOCEPHALUS* (CLADOCERA)

BY

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

# ANALYSIS OF THE GENETIC COMPONENT OF LIFE HISTORY PARAMETERS USING LABORATORY-REARED *SIMOCEPHALUS* (CLADOCERA)

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Laboratory rearings of field-collected, cloned *Simocephalus exspinosus* provided data that do not support the r- and K-selection model. A shift from r-selected to K-selected characters was not observed in a temporary pond population initially subjected primarily to density-independent mortality factors and later, as the pond decreased in size, to increasingly greater density-dependent mortality factors. The life history features of animals sampled throughout this period remained nearly constant. These results are consistent with data from laboratory rearings that indicated that some clones were of superior fitness over all food concentrations tested.

*Simocephalus exspinosus*, *S. vetulus*, and *S. serrulatus* populations appear to respond to nonvisually-oriented predation by increased

age-specific size, increased age-specific fecundity, and increased intrinsic rates of natural increase ($r_m$) and respond to visually-oriented predation by decreased size at first reproduction, decreased age-specific size, decreased $r_m$ values, greater body pigmentation, and smaller eyespot-body size ratios.

Interspecific differences in life history parameters and habitat preferences were observed among the three species by means of field collections and laboratory rearings. *Simocephalus exspinosus*, which inhabits primarily temporary ponds, has the greatest age-specific size, smallest size-specific fecundity, and largest size at first reproduction. *Simocephalus vetulus*, which inhabits both temporary and permanent ponds, has the smallest age-specific size, largest size-specific fecundity, and smallest size at first reproduction. *Simocephalus serrulatus*, which inhabits primarily permanent lakes, has the lowest age at first reproduction and showed no evidence of males and ephippial females, which were occasionally seen in the other species.

# INTRODUCTION

*Simocephalus* are large (less than 3.5mm) cladocerans of the family Daphnidae that are abundant in many bodies of water in north central Florida during the winter and early spring. Three species, *S. exspinosus* Koch, *S. vetulus* O.F.M. and *S. serrulatus* Koch, can be found in a wide variety of habitats ranging from small bathtub-size puddles to the large natural lakes of the area. Unlike most of the Daphnidae commonly studied, they are benthic, i.e. they are associated with substrates such as vegetation and sediment surfaces. These cladocerans are quite useful in ecological studies for several reasons. *Simocephalus* are easy to collect in large numbers with a minimum of equipment. The variety of habitats they inhabit allows researchers to collect from allopatric populations of the same species that have been subjected to different selective pressures. Each species can be collected in sites containing only one species as well as sites containing two species, thus allowing both interspecific and intraspecific comparisons. *Simocephalus* are large enough to be seen with the unaided eye, greatly simplifying their handling, but are small enough to be reared in large quantities in a small space. Reproducing primarily by mitotic parthenogenesis, they can be cloned in the laboratory, allowing

the maintenance of lines for long periods and the accurate measurement of the phenotypic variability of a genotype.

*Simocephalus* were used to examine several ecological questions. Some assumptions of the r- and K-selection model (MacArthur and Wilson 1967) were tested using *S. exspinosus* from several different habitats. The model predicts that populations subjected to predominantly density-independent (D.I.) mortality factors would have different life history tactics than those subjected to predominantly density-dependent (D.D.) mortality factors. Individuals in populations under D.I. control should be r-selected, producing a maximum number of offspring without regard to competitive ability. Populations under D.D. control would contain K-selected individuals that would produce more competitive but fewer young. A continuum exists between extreme r-selection and extreme K-selection with numerous correlates associated with each end (Pianka 1970). As the importance of D.D. factors increase relative to D.I. factors, K-selected characters should become more favored by natural selection than r-selected characters. A tradeoff should occur between the two ends of the continuum for the effects of r- and K-selection are opposite (Gadgil and Bossert 1970). An organism adapted to r-selection should show reduced fitness under K-selected conditions and vice versa.

Evidence for this predicted tradeoff was sought in two ways. *Simocephalus exspinosus* from one temporary pond were cloned and reared under controlled conditions. Individuals collected soon after the pond filled would most likely have been under D.I. control and thus should show r-selected characteristics: high $r_m$

values, small age-specific size, high age-specific fecundity, high size-specific fecundity, small age at first reproduction, small size at first reproduction, and high relative growth rates. As the pond dried and the population increased toward the carrying capacity, D.D. factors would most likely have become more important, favoring the individuals that possessed relatively K-selected characteristics: low $r_m$ values, large age-specific size, small age-specific fecundity, low size-specific fecundity, large age at first reproduction, large size at first reproduction, and low relative growth rates. Measurements of these parameters were taken from animals collected on six dates from January 15 until March 27, enough time for approximately 10 generations of *S. exspinosus* (Table 5), to see if the expected tradeoff occurred. The relationships between age of parents and size of their eggs and young were examined to determine whether the manipulation of egg and young size could be used for regulating reproduction at various ages.

For further evidence, a food experiment was conducted to determine whether clones with high rates of increase (r) at high food levels had lower r values at low food levels than clones with low r values at high food levels. Three clones were reared under six different food concentrations to see whether this tradeoff would occur. Since food supply per individual in natural populations would most likely be inversely proportional to population density, varying food levels should allow indirect examination of the effects of population density on r values.

Another subject of ecological concern is the reaction of prey species to visual and nonvisual predation. Numerous investigators have reported increased predator avoidance by the evolution of changes in size, body shape, and pigmentation by cladocerans and other members of the plankton (Confer and Blades 1975; Dodson 1970, 1972, 1974a,b; Hairston 1979a,b; Hutchinson 1967; Kerfoot 1974, 1975, 1977a,b, 1978; Kerfoot and Peterson 1980; Mellors 1975; O'Brien and Vinyard 1978; O'Brien et al. 1979; Sprules 1972; Werner and Hall 1974; Zaret 1972a,b; Zaret and Kerfoot 1975). The tactics used by the more benthic cladocerans, such as *Simocephalus*, have not received the same attention. Intraspecific comparisons of life history traits, morphology, and pigmentation of two populations of *S. exspinosus*, one subjected to very little predation of any kind and the other subjected to heavy fish predation, are made from both laboratory-reared and field-collected animals. Laboratory observations confirm that two species of fish, *Gambusia affinis* and *Heterandria formosa*, commonly found in the same sites as *Simocephalus*, readily ingest *Simocephalus*. In addition, comparisons of laboratory rearings and field collections of animals from a variety of habitats provide insight into the interspecific and intraspecific trends induced by various types of predation.

The third major part of this investigation is a comparison of some of the ecological characteristics of the three species. The key identifying characters, the habitat preferences, and differences in growth rates and life history strategies are examined. Life history traits were determined through laboratory rearings while the key characters were examined using field-collected specimens.

## METHODS

A consistent rearing method that can be duplicated over long periods and that allows uniform growth, survival, and reproduction is needed to study the life history features of cladocerans. Such a method used while examining the life history tactics of *Simocephalus* populations at different times in the same temporary pond has five major components (White 1981).

Food--Unialgal cultures of the unicellular green alga *Stichococcus bacillaris* Nag obtained from a contaminated flask of culture medium provided a consistent and easily quantifiable source of food that met the nutritional requirements of the cladocerans. Algal cultures were grown under cool white fluorescent lights in 2 l flasks containing Bold's Basal "3N" growth medium (Bold 1967). The flasks were plugged with cotton through which glass tubes extending into the liquid were inserted. Filtered air was pumped through these tubes to aerate and agitate the cultures.

*Simocephalus* were provided with algal cells at a concentration of 500,000 cells/ml, which apparently provided a superabundant food supply. Hutchinson (1967) reported that *S. vetulus* reaches a plateau of feeding efficiency at food concentrations between 250,000 and 500,000 cells/ml. Food was prepared each day by counting the individual cells in a known volume of algal stock with a hemocytometer and diluting this stock to the proper concentration.

Water--Water was conditioned by passage through two 110 l aquaria. Tap water was introduced into the first tank, which contained numerous small fish, a large population of snails, and a dense growth of *Vallisneria*. A fluorescent light in the hood was kept on continuously, and the 568 l/hr motor driven filter was cleaned every week. Water was siphoned from this tank to another unilluminated one that contained a few fish and snails but no plants. This aquarium had both an undergravel filter and a 568 l/hr motor driven filter. Water from the second aquarium was placed in 7 l flasks and autoclaved for 15 min at 121° C under 1,520 mmHg. Taub and Dollar (1968) reported that autoclaved culture water boosted survival and reproduction in *Daphnia pulex*. After cooling overnight, the water was mixed with the algal stock and used.

Temperature--Experimental cultures were reared at 27° C. Other cultures raised at 20° C and 30° C indicate that this setting is within the tolerance range of *Simocephalus*.

Light--An illumination schedule of 12 hr light and 12 hr dark was maintained. Animals reared under 24 hr of light did well, while those raised in complete darkness usually died, indicating that some light is important.

Rearing tests--Collections were made in the field with a white pan and an eye dropper. The pan was dipped into the water among vegetation or slightly above the bottom and then placed on a level surface. *Simocephalus* were removed from the pan individually with an expanded eye dropper and placed into a vial for transport to the laboratory. Each field-collected animal was isolated and subjected to the rearing conditions. These individuals were allowed to

reproduce at least three times in the laboratory, after which young were isolated and the field-collected individuals discarded. These young were allowed to reproduce at least three times, after which young were again isolated and the parents discarded. These young were used in the experiments. Each individual was kept in its own container, a 220 ml capacity plastic cup containing 60 ml of the diluted algal culture. These cups were kept on white trays in an environmental chamber. Each day the contents of the cup were poured into an illuminated 76 mm glass culture dish, the cladoceran was transferred with an expanded eye dropper to a duplicate cup containing fresh food, and the newborn were collected by pouring them into a 74 micron sieve. Offspring from clones of 10 siblings were collected on the sieve, washed into a plastic pill vial, killed with 10% formalin, and counted at 12 power with a dissecting microscope. Body lengths were measured at 24 power using a dissecting microscope with a measuring eyepeice. Algal build-up was removed from the sides and bottom of the culture cups each week.

Evaluation of Method-- Three questions must be considered before confidence can be placed in the technique. Does it allow high rates of survival and reproduction? The survival rates to age 14 days of clones of *S. exspinosus*, *S. vetulus*, and *S. serrulatus* are in Table 1, and the mean intrinsic rate of natural increase, $r_m$, for the same clones are in Table 2. These tables indicate that the method allows high rates of survival and reproduction. In addition, comparisons between field-collected and laboratory-reared specimens show that size-specific fecundity was

consistently greater in the laboratory-reared animals (Table 3A-I). Does the method allow consistency over a long period of time? In Table 4, body lengths at age 14 days and $r_m$ values of specimens from January and April cohorts of the same clones indicate that consistency is maintained. Does it allow consistency between parents and offspring? For 10 parent-offspring pairs, a paired comparison "t" test showed no difference between the total number of young produced by age 14 days ($0.4 > p > 0.2$) or between the body length at age 14 days ($0.9 > p > 0.5$).

The food experiment used the same method with some modifications. Food concentrations of 1,000,000, 500,000, 250,000, 50,000, 5,000, and 0 cells/ml were used. The 1,000,000 cells/ml concentration was made first each day by the use of the hemocytometer. Other food levels were achieved by dilution of the concentration. The autoclaved aquarium water was filtered through a 0.47 micron millipore filter to assure that the algal cells, added later, were the main source of food. Three clones were used for the study, each chosen for its $r_m$ value from a previous rearing. Eight members of each clone were reared at each food level. All individuals were measured each day, and the young from each animal were counted as they were removed from the illuminated culture dish with an eye dropper.

The rearings used in the comparison of the three species also employed the same techniques with slight alterations. Each field-collected specimen was represented by only one animal in the laboratory rearings. This provided for a measure of variability in the population but not in the individual genotype. All animals

were measured each day, and the young were counted as they were removed from the culture dish with an eye dropper.

To determine the relationship between the size of the young and the age of the parent, newborn from adults of known ages were measured under a 24 power dissecting microscope. All the young of the first brood were measured, and 5 young were measured at random from later broods. If shed skins were evident, indicating that the young had molted, animals of that brood were not measured. For this determination, several individuals were reared for as long as 33 days instead of the usual 14 days.

To see if the size of the eggs changed with the age of the parent, specimens from 4 clones were reared using the standard method for as long as 25 days. Individuals from the clones were killed and stripped of eggs when the eggs were seen to be at the correct stage of development. All eggs unbroken during removal were measured along the long axis under a 100 power dissecting microscope.

To determine growth rates of each species of *Simocephalus*, knowledge of the relationship between body length and weight was required. Laboratory-reared animals were measured under a 24 power dissecting microscope, dried in a 60° C drying oven for 2 days, and weighed on a Cahn G-2 electric balance to yield equations that would predict the dry weight from body length of the living animals. Four equations were used: (*S. vetulus*) $\log_{10}X = 2.90 \log_{10}Y - 6.08$; (*S. serrulatus*) $\log_{10}X = 3.07 \log_{10}Y - 6.35$; (Pine Pond *S. exspinosus*) $\log_{10}X = 3.60 \log_{10}Y - 7.18$; and (other *S. exspinosus*) $\log_{10}X = 4.65 \log_{10}Y - 9.04$; where X is the dry weight in milligrams, and Y is the length in measuring eyepiece units (0.0378 mm).

Some data were obtained from field-collected organisms. These animals were transported live to the laboratory where they were killed

in dilute alcohol and immediately examined under a microscope. The length, the number of eggs, presence of spinules on the vertex, shape of the ocellus, size of the eyespot along the longest axis, and the pattern of spination on the postabdominal claw were recorded for most individuals. Some animals were measured only for length, number of eggs, and degree of pigmentation on the shell. Pigmentation was measured using a rating system of from 1-5.

1= no pigmentation in the shell

2= shell with a few scattered patches

3= shell with a distinct pattern of pigmentation

4= pigmentation over most of the shell

5= pigmentation over the entire shell

The red tinge common in *S. exspinosus* from highly stained water was not considered to be pigmentation in the shell.

The bulk of the data was analyzed using programs of the Statistical Analysis System (S.A.S. 1979) and the Northeast Regional Data Center computer in Gainesville, Florida. Analyses of variance were performed using the general linear model procedure. The Duncan Multiple Range test was used to determine the location of significant differences among 3 or more means. Labels of means not significantly different from each other at the .05 level are joined by an underline in the tables. For the food experiment, differences among the slopes and y intercepts of the 3 lines formed by plotting r against $\log_{10}$ food concentration were examined using analysis of covariance. Pigmentation rankings were subjected to the nonparametric one-way analysis procedure that included parametric one-way analysis of variance and Kruskel-Wallis K-sample tests.

A paired-observation t-test contained on a Monroe 344 calculator was used to analyze eyespot size data.

Growth data fit the logistics growth model (Ricklefs 1967), allowing relative growth rates to be calculated using the methods of Crossner (1977).

Values of r and $r_m$ were calculated on a Tektronix 31 programmable calculator using the equation $1 = \Sigma\ e^{-r_m x}\ l_x\ m_x$.

Collection Sites--The Archer site is found at the southeast corner of Old Archer Road and S.W. 23rd Street in Gainesville, Florida. It is an unshaded, unstained drainage ditch no greater than 1.5m wide and no greater than 0.5m deep. The ditch floods to a length of about 100m during a heavy rain but holds water for only about 15m of its length for any extended period. One end of the ditch accepts water runoff from a University of Florida livestock rearing complex, and the other end empties into a drainage culvert. The ditch experiences unidirectional flow during and for a short time after a heavy rain. The bottom of the culvert is above the bottom of the ditch, allowing a puddle of standing water to remain. The size and depth of this puddle remain fairly constant during the winter months due to the maximum size limit imposed by overflow into the culvert and to frequent fillings from rain during this wet time of the year. Being in a flow-through system, the flora and fauna in the ditch are subjected to frequent washouts. In 1978, 1979, and 1980 the site first filled in early January and contained water until the first week in April. Washouts were frequent in January and February but became rare in March. The site occasionally filled during other seasons but did not hold water for extended periods. No attempt was

made to identify all the fauna in the ditch, but observations made while collecting showed that the site contained copepods, ostracods, amphipods, small Cladocera, Ephemeroptera nymphs, Odonata nymphs, Diptera larvae, Coleoptera larvae and adults, Hemiptera, *Rana* tadpoles, *Bufo* tadpoles, *Hyla* tadpoles, but no fish. Ostracods, *Simocephalus*, and small cladocerans were observed in very large numbers during the wet winter months, but the populations dwindled somewhat as the pond began to dry. The bottom of the pond was covered with submerged vegetation and some emergent vegetation. *Simocephalus exspinosus* was the only *Simocephalus* collected at this site. Archer was selected for an examination of the r- and K-selection model for it is an exposed, unstained, fishless, temporary pond that would have *S. exspinosus* subjected to heavy D.I. selection due to the frequent washouts and to intense D.D. selection later as the pond dried and the washouts no longer occurred.

The Pine site is found on the east side of S.W. 6th Street between South Main and Waldo Road in Gainesville. It is a shaded pond about 50m long and 30m wide that receives overflow from a creek flowing into Payne's Prairie. It experiences no unidirectional flow during rains, and its depth, 1.5m at most, varies with the weather. The pond holds water for most of the year but does dry occasionally. The water is darkly stained, and the bottom is covered with dead leaves, allowing few submerged plants to grow, although there are a few emergents present. Invertebrates are scarce, but small fish are abundant and could easily invade from the nearby branch. Both *S. exspinosus* and *S. vetulus* were found at this site

although neither was ever very abundant. This site was chosen for the predation studies as an example of a small, semipermanent, shaded, darkwater pond with heavy fish predation.

Mount Vernon Pond is located north of Archer Road about 100m northeast of the Archer site. It is a shaded, darkwater, temporary pond with dead leaves covering the collection location. Part of the pond has submerged and emergent vegetation, but the sample area has neither. The pond is 20m in diameter and less than 0.5m deep. Invertebrates are very common, and fish have been seen in parts of the pond, but never in the collection area. The pond does dry regularly, and fish *(Gambusia affinis)* are probably introduced on an irregular basis. *Simocephalus exspinosus* was the only species collected at this site.

Tennis Court Pond is a small, shaded, darkwater, temporary pond located in the McPherson Center in southeast Gainesville. This pond is one of the most ephemeral of those sampled. It has a bottom covered with leaves and very little emergent vegetation. Since it is an undrained depression, its size fluctuates with the amount of rain. Normally it is about 5m by 10m and 0.5m deep, although it can flood to a size of 15m by 30m. Invertebrates are plentiful, but no fish are present. *Simocephalus exspinosus* was collected at this site.

Santa Fe Pond is located on Santa Fe Community College campus in northwest Gainesville. It is a manmade pond 50m in diameter and 5m deep that receives runoff from the campus. It is unshaded over most of its area, and the water is not stained. A small fringe

of submerged vegetation exists around the edges, but the bottom lacks vegetation in deeper water. Invertebrates are common, but fish are absent. The pond holds water for most of the year but does dry occasionally. *Simocephalus exspinosus* was collected at this site.

The smallest collection site is called the Puddle. It is located in the Lochloosa Wildlife Management area 5m from the northwest corner of the Still Hunt Pond site. It is a shallow depression around an old stump and is 1m by 2m and 0.25m deep. Water from a nearby drainage ditch may seep into it during a heavy rain, but it is quickly isolated from the ditch once the rain stops. The bottom is covered with submerged vegetation, and some emergents grow around the stump. The area is unshaded, and the water in the Puddle is not stained. Invertebrates are common, and *Bufo, Hyla,* and *Rana* tadpoles are often present. No fish are present, but *Ambystoma*, a known visual predator on cladocerans (Anderson 1968; Brophy 1980; Dodson 1970, 1974a; Hairston 1979a; Sprules 1972), have been collected in Still Hunt Pond a few meters away. Although Puddle and Still Hunt are close to each other, separated by a slight rise, they are not connected during heavy rains, and Puddle contains *S. exspinosus* while Still Hunt contains *S. serrulatus*.

Still Hunt Pond is located just north of S.R. 346, 3km east of the River Styx Bridge. It is a permanent lake 200m by 150m with a depth of less than 2m. The surface is covered with emergent and submerged vegetation. Although invertebrates are

abundant and amphibians are quite common, no fish have ever been observed. *Simocephalus serrulatus* was collected at this site.

River Styx Pond is a small permanent pond located on the north side of Alachua County Road 234 500m east of the bridge across Camp Canal (River Styx). The pond, 20m by 50m and less than 2m deep, is filled with submerged and emergent vegetation and is heavily stained. Invertebrates are common, and fish are present. The site is unshaded over most of its surface. *Simocephalus serrulatus* was collected from this site.

The River Styx Bridge site is located at the northeast corner of the S.R. 346 bridge over the River Styx, a flowing darkwater stream connecting Newnan's Lake and Orange Lake. This section is usually choked with submerged, emergent, and floating vegetation. Invertebrates are present, and fish are abundant. *Simocephalus serrulatus* was collected there.

Stock Pond is located in Lochloosa Wildlife Management Area 200m north of S.R. 346 about 1km east of the River Styx Bridge site. It is a semipermanent pond 100m by 50m and less than 1m deep. Submerged and emergent vegetation cover the bottom, the site is unshaded, and the water is not highly stained. Invertebrates are quite abundant, amphibians are common, but fish are absent. *Simocephalus serrulatus* was collected in Stock Pond.

Biven's Arm is a pair of eutrophic lakes in south Gainesville that drain into Payne's Prairie. The two lakes are separated by U.S. 441 although a culvert under the road connects them. The

collection site is in the downstream lake near the culvert leading from the upper lake. The lower lake is usually covered with emergent and floating vegetation, although spraying of herbicides in the winter of 1980 reduced the vegetation. No *Simocephalus* were collected after the spraying. Before the spraying, however, both *S. serrulatus* and *S. vetulus* were abundant, as were other invertebrates. Fish were always present.

Lake Alice is located on the University of Florida campus and receives the effluent from the University sewage treatment plant. Most of the lake is choked with vegetation, but an area 300m by 150m is open. Samples were taken near emergent vegetation bordering the open area. Invertebrates are quite common among the vegetation, but fish are also present. *Simocephalus vetulus* was collected at this site.

Psychology Pond is a small, temporary, shaded, unstained, manmade depression near the Psychology building on the University of Florida campus. It is 10m by 15m and no more than 1.5m deep. The surface is generally choked with emergent and submerged vegetation. Both *S. vetulus* and *S. exspinosus* have been collected at this pond at the same time, although *S. vetulus* may have been recently introduced from Lake Alice by ecology classes.

Austin Carey Pond is located in the Austin Carey Memorial Forest northeast of Gainesville. It is a small pond, 15m by 30m and 1.5m deep, constructed for research on the white amur. Its water level is manipulated by the researchers as is its crop of submerged vegetation. Invertebrates are present, and fish, in addition to the white amur, are common. *Simocephalus vetulus* was found in this pond.

## RESULTS

The mean $r_m$ values for the 6 cloned laboratory rearings from the Archer site and the results of the analysis of variance of the means (Table 5) show that the trend towards a lower $r_m$ with the increased importance of D.D. mortality factors did not occur. No significant difference was seen among the rearings. Other life history parameters also showed no trends. Size at first reproduction (Table 6), age at first reproduction (Table 7), and size of newborn (Table 8) showed no significant differences among the rearings. The differences in death rates (Table 9) and growth rates (Table 10) did not follow any pattern. The significant differences seen in the m(x) values (Tables 11A and B) showed a lack of predictable trends, with the last rearing having the consistently highest age-specific fecundity, contrary to the prediction of the model. Age-specific size (Tables 12A and B) showed similar results. The last rearing consistently had the largest individuals, frequently followed by individuals from the earliest cultures.

The relationship between the age of parent and egg size (Table 13) indicates that egg size remains constant as parents grow older. The comparison of the size of the young from parents of different ages (Tables 14A-E) indicates that newborn young are smaller from early reproductions but their size stabilizes quickly as the parent matures.

The results of the food experiment did not conform to the predictions of the model. The r values for the Archer clone, the Pine clone, and the Puddle clone, hereafter known as A, B, and C, used in the food rearings did, however, reveal a trend (Table 15). A and B showed higher rates of increase at both high and low food levels than did C. C did not reproduce at all at the lowest level while A and B were able to reproduce in water passed through a 0.47 micron filter. As food level increased, C continued to have inferior reproductive success, never reaching the high rates of increase attained by the other clones. Plots of r against $\log_{10}$ food concentration (Table 15, Figure 1) show that the lines for A and B are not significantly different from each other. The line for C, however, is significantly different from B's line with regard to y intercept. Although the slope is greater and the y intercept smaller for C's line than for the others', the lines never cross due to C's lower r values at high food levels. This indicates that C is more sensitive to food levels and is unable to tolerate low levels or exploit fully high concentrations. A and B, on the other hand, are more flexible and can maintain a relatively high fitness over all tested food concentrations. This flexibility can be seen by examining several life history parameters. Each clone is examined relative to each other clone with regard to size-specific fecundity (Table 16A-F), age-specific fecundity (Tables 17A-F), age-specific size (Tables 18A-F), size at first reproduction (Table 19), and age at first reproduction (Table 20). Growth rates and death rates are found in Tables 21 and 22.

A-B: Size-specific fecundity--B was consistently greater than A. This was probably due to the smaller size of young in B.

Age-specific fecundity--A tended to have greater fecundity at food levels 50,000 cells/ml and above while B produced more at lower concentrations. At levels of 1,000,000 to 50,000 cells/ml A produced more young 26 times (9 significant) while B produced more 12 times (5 significant). A had greater fecundity only once at the 5,000 cells/ml concentration while B was more productive 4 times (1 significant). B always produced more young at the lowest food level.

Age-specific size--A was consistently larger. Differences were significant through the 500,000 cells/ml food level but increasingly less significant as food decreased.

Size at first reproduction--A always started reproduction at a larger size than B.

Age at first reproduction--B reproduced at a significantly older age than A at the highest food level. The opposite was true at the two lowest levels. Differences were not significant at other concentrations.

A-C: Size-specific fecundity--A and C were not significantly different at high food levels, but as food decreased A produced significantly more young than C.

Age-specific fecundity--The trend was for A to have more young per day than C. A's fecundity was greater 37 times (8 significant) while C's was greater 7 times (3 significant).

Age-specific size--At low food levels the two clones were not significantly different, but as food increased A was able to increase growth more than C, becoming significantly larger than C at the highest food level.

Size at first reproduction--The size did not decrease for C as food increased. A's size did, being larger than C's at the two highest food levels and decreasing below C's at the lower concentrations.

Age at first reproduction--A always produced earlier than C.

B-C: Size-specific fecundity--B was always more productive than C.

Age-specific fecundity--The trend was for B to be more productive, being more fecund 25 times (3 significant), while C was more fecund 11 times (2 significant).

Age-specific size--C was constantly larger than B.

Size at first reproduction--C always started reproducing at a larger size than B.

Age at first reproduction--C was always older than B.

Summarizing, one sees that B always had the greatest size-specific fecundity. A and C were about the same at high food levels but C showed a much greater reduction as food levels dropped. Age-specific fecundity was lowest at all levels for C. A outproduced B at high food concentrations and vice versa at low levels. B had the smallest age-specific size. A was significantly larger than C at high food levels but became similar in size at low concentrations, sacrificing

growth for reproduction. C always had the greatest age at first reproduction. A produced before B at high food levels and after B at low levels. B always started reproduction at the smallest size. A first produced young at a larger size than C at high food and at a smaller size than C at low concentrations.

The effects of visual versus nonvisual predation were examined by comparing *S. exspinosus* from a site with fish, Pine, to conspecifics from a site without fish, Archer. Pine individuals had a lower $r_m$, started reproduction at an insignificantly smaller size, reproduced at an insignificantly older age, and had larger relative growth rates than Archer individuals (Table 23). Pine individuals were significantly smaller at all ages (Table 24). Size-specific fecundity was not significantly different between the two populations (Table 25). Pine animals tended to have lower age-specific fecundity, being less fecund 9 times (1 significant), while Archer was less fecund 3 times (1 significant) (Table 26). Pine specimens were more heavily pigmented than Archer specimens (Table 27). The results from pigmentation measurements of other species and populations are included in Table 27.

The relationship between eyespot size and body length of *S. exspinosus* was examined in one habitat with no visually-oriented predation, Archer, and in 3 habitats with such predation, Mt. Vernon, Puddle, and Pine Ponds. Visually-oriented predation is slight and very sporadic in Puddle and Mt. Vernon Ponds but is heavy in Pine Pond. Identically-sized individuals collected from Archer and each of the other sites were randomly matched, and differences in eyespot

sizes for several arbitrary body size classes of all field collected specimens are listed in Table 28. The subsamples utilized in the t-test clearly established that specimens of *S. exspinosus* from Archer had larger eyespots than those of identical sizes from Pine Pond (29 pairs, $p < 0.05$), Mt. Vernon Pond (39 pairs, $p < 0.0005$), and Puddle (36 pairs, $p < 0.025$). In addition, no significant differences were noted in paired observation t-tests involving all possible combinations of Mt. Vernon, Puddle, and Pine Ponds.

A correlation analysis (Sokal and Rohlf 1969) between the $\log_{10}$ of eyespot size and the $\log_{10}$ of body length yielded correlation coefficients of 0.80-Archer, 0.85-Pine Pond, 0.93-Mt. Vernon Pond, and 0.85-Puddle. The slopes of the principal axes were 0.79-Archer, 0.76-Pine Pond, 0.70-Mt. Vernon Pond, and 0.66-Puddle. A slope of less than 1.00 indicates that the $\log_{10}$ of eyespot size changes at a lower rate than does the $\log_{10}$ of body length. For values less than 1.00, the lower the slope, the greater is the difference between the rates of change of eyespot and body sizes. Zaret and Kerfoot (1975) suggest that the value of the slope may be inversely related to the degree of eyespot size-selective predation. These results appear to confirm this suggestion since the dimensions of Archer specimens produced a higher slope than did those of the other 3 ponds' specimens.

Comparisons between field collected and laboratory-reared animals are found in Tables 3A-I. These tables must be used carefully for the growth rates in the field are probably not the same as in the

laboratory. The ages of field-collected animals cannot be determined with the present data. Also, the field collections do not represent the population in a random fashion. The tables do imply that individuals in sites without abundant visual predators could and did grow to a larger size, presumably due to the lack of heavy size-selective visual predation.

Ecological differences among the three *Simocephalus* species can be seen by examining life history parameters. Age-specific size was significantly different among the species (Table 29, Figure 2), *S. exspinosus* being the largest and *S. vetulus* the smallest. Relative growth rates (Table 21) were highest for *S. vetulus* and lowest for *S. exspinosus*. Size-specific fecundity was significantly different for most sizes (Table 30, Figure 3), with *S. vetulus* having the greatest values and *S. exspinosus* the smallest. Age-specific fecundity values were rarely different among the species (Table 31, Figure 4). *Simocephalus serrulatus* tended to be more fecund, having the highest values 9 times (1 significant). *Simocephalus exspinosus* values were greatest 3 times (1 significant) while *S. vetulus* were never the most fecund. No significant differences were found among the $r_m$ values (Table 32). Age at first reproduction was significantly smaller for *S. serrulatus* than for the others (Table 33). Size at first reproduction was significantly different among the species (Table 34) with *S. exspinosus* reproducing at the largest size and *S. vetulus* at the smallest. Death rates (Table 35) were somewhat higher for *S. exspinosus* than for the other species. An overview

reveals that the 3 species attain similar rates of increase through different tactics. The temporary pond species, *S. exspinosus*, grows quite large, produces the fewest but largest young at any given body size, and begins reproduction at the largest size. The permanent lake species, *S. serrulatus*, is slightly smaller, produces more but smaller young at a given body size, and starts reproduction at the earliest age. *Simcephalus vetulus*, found in both types of habitats, is the smallest species, produces the most but smallest young at a given body size, and starts reproduction at the smallest size.

Intraspecific interhabitat comparisons of life history parameters are found in Tables 36A-40B. Differences seen among habitats for *S. exspinosus* seem to be due to distinct differences in predation pressures. Three habitats tend to be most highly affected by non-visual predation, Tennis Court Pond, Santa Fe Pond, and Mt. Vernon Pond. Two populations, Puddle and Pine, show the influence of heavier visual predation. The Archer population has practically no predation of either kind. Visually-oriented predation causes a shift towards individuals with smaller age-specific size ($p < .0001$ after day 2, Tables 36A and B), smaller age-specific fecundity (Table 37A and B), and smaller size at first reproduction ($p < .0001$, Table 38). The trends are reversed for populations subjected to nonvisually-oriented predation, and the values for Archer are generally between the two extremes. No consistent trends are evident for age at first reproduction (Table 39), or size-specific fecundity (Table 40A and B).

The situation for *S. vetulus* and *S. serrulatus* is not as clear. The relationship between visual and nonvisual predation is not obvious since both types of predators are present in most habitats. Since traits often respond in different ways to different types of predation, only those traits, such as pigmentation, that are affected by only one type of predation should be compared among sites where the relative importance of opposing selective pressures is not obvious.

The pigmentation results for *S. vetulus* and *S. serrulatus* are similar to those of *S. exspinosus* (Table 27). A significant difference was seen between *S. serrulatus* from River Styx Bridge, a site with abundant fish, and those from Stock Pond, a site with few visual predators and abundant invertebrates. In *S. vetulus*, Psychology Pond had the lightest specimens. This site has no fish or abundant invertebrate predators. The darkest specimens came from Pine Pond, a site with abundant fish and few invertebrates. Specimens from Lake Alice, a lake with an abundance of both types of predators, were intermediate with regard to pigmentation.

## DISCUSSION

The r- and K-selection model (MacArthur and Wilson 1967) is often used to predict trends in the evolution of life history parameters. Its basis is found in the realization that an individual may be placed in a habitat with abundant resources and no intraspecific competition. The reproductive tactics that would best insure maximum attainable fitness, the production of the maximum number of reproductively successful offspring, for that individual should be different from those of an individual in a descendant population existing at the carrying capacity of the habitat for that species. This research tests the model by examining the reproductive tactics of clones taken from the same continuous natural population subjected to both extremes at different times. A continuum exists between the two extremes, and numerous correlates are associated with each end (Pianka 1970). Genotypes that are most fit at the r (D.I.) end would be least fit at the K (D.D.) end of the continuum and vice versa. As assumption central to the model is that a genetically controlled tradeoff of traits should occur in the population as D.I. selection was replaced by D.D. selection. Numerous investigators have tested the validity of the model with a variety of organisms. Stearns (1976, 1977) reviewed much of the data and critiqued the model, reminding researchers ". . .that the interpret-

ation of data is ambiguous because the theory is incomplete." (Stearns, 1977, p. 146) Good empirical data, however, must be available if theorists are to form a realistic life history theory.

Stearns (1977) used six criteria to examine the reliability of life history data.

A. "Did the author rear the organisms under constant conditions to isolate the genetic component of the variability observed in the field?" All *Simocephalus* for the examination of the r- and K-model were obtained from animals reared under constant laboratory conditions.

B. "Did the author attempt to measure the environmental factors later invoked to explain differences in reproductive traits?" For clones reared to observe changes in $r_m$, no numerical values were placed on competition, crowding, or other selective factors in the natural habitat, but relative differences were described. Population estimates were not made for they would be of little use in determining competition levels unless food concentrations were known. Food availability would be difficult to determine accurately because the complete diet of *S. exspinosus* is not known. Counts of algal cells and bacteria would give poor estimates of food supplies because some large or filamentous algal cells would be unusable by the cladoceran, and the lower size range of usable particles is quite small. *Simocephalus exspinosus* have grown and reproduced in autoclaved aquarium water passed through a 0.47 micron filter. For this study the obvious long-term trends provided a more reliable description of the environmental factors than a series of necessarily inaccurate estimates. Numeric values would be essential if comparing different

populations in different habitats but would not be vital when dealing with one habitat in which observable changes did occur. Numeric values were placed on the factors examined in the food experiment.

C. "Did the author attempt to measure the degree of density-dependent or density-independent regulation?" As seen in "B," relative measures were used.

D. "Did the author attempt to measure year-to-year variabiltiy in the mortality schedule?" The laboratory cloned rearings had accurate measurements of mortality schedules, and the rearings of several genotypes provided a measure of variability in the population. The year-to-year variability is not important in this study that examines variability in a population on a smaller time scale. Variability within a clone was measured in the food experiment by replicate rearing of members of the same clone.

E. "Were the statistics convincing? For intraspecific comparisons were analyses of variance or covariance done?" Analysis of variance was the statistic used most often on the data.

F. "Was an attempt made to measure reproductive effort?" Reproductive effort was measured as number of young age-specifically and size-specifically. Relative differences between rearings with regard to the comparison of number of young versus amount of growth would give reliable information concerning the proportion of the total intake that went to reproduction as opposed to growth. The number of young is a reliable index of reproductive effort over most of the parents' lifespan for the size of the young remains quite constant after the very earliest of reproductions.

Perhaps the most crucial of the six criteria is "A." Unless differences in life history tactics that determine the fitness of an organisms are genetically controlled, natural selection cannot affect future populations. If the different test organisms are not reared under identical conditions to insure that the only variable is genetic, one does not know whether differences between organisms in the field are but reflections of phenotypic plasticity. Most workers have not examined this aspect (Stearns 1977), assuming that variability was genetically based. Several workers have rigorously tested, with varying results, for the genetic component of the variability found in different populations of the same species. Gadgil and Solbrig (1972) and Solbrig and Simpson (1977) lent support to the model by rearing dandelions (*Taraxacum*) in greenhouses and in garden plots. Genetic differences in competitive and reproductive ability were seen that suggested the predicted tradeoff in adaption to r- and K-selection. No tradeoff was seen, however, in a study of *Escherichia coli* by Luckinbill (1978). Instead, one genotype was seen to be superior to another during both D.I. and D.D. control.

This study of *S. exspinosus* examined the genetic component of variability among temporally separated populations by rearing the organisms under identical conditions. The cloned rearings of *S. exspinosus* from the Archer site during the winter of 1979 did not show the tradeoff predicted by the r- and K-selection model. The model predicts that the populations present during times of

heavy D.I. mortality would have high $r_m$ values. Heavy D.I. mortality occurred from the time of the pond's filling in early January until the pond no longer experienced regular washouts in early March. As the pond began to dry, D.D. factors became increasingly important, and $r_m$ values should have dropped. Contrary to the predictions of the model, the $r_m$ values for rearings at six dates between January 15 and March 27 showed no significant difference. The highest $r_m$ values were actually obtained on March 27, two days before the pond dried.

Other life history parameters also indicate that the expected tradeoffs did not occur. Among the six dates there was no significant difference for size at first reproduction, age at first reproduction, or size of newborn. Neither growth rates nor death rates showed any trend. The m(x) values showed no significant differences for most days, but when they did, March 27 clones always had the highest values, contrary to the model's predictions. Age-specific size measurements showed that, as expected, March 27 individuals grew to the largest size, but the January specimens were generally the next largest, contrary to what would be expected.

Is the shift from D.I. to D.D. selection realistic in this site? Several things must be considered when dealing with this question. The morphometry of the pond is such that washouts are common during the rainy seasons. Water flows through the ditch into a culvert, removing flora and fauna from the ditch. Runoff from the hog farm would be high in nutrients. As a result, the population of *S. exspinosus* would be reduced, and fresh water rich in nutrients

would be introduced at frequent intervals, keeping the cladoceran population below carrying capacity and stimulating the growth of algae and bacteria. Predation, a problem that could cloud the results, does not seem to have a great effect on any size of *S. exspinosus* in Archer Pond. Predation by fish is nonexistent, and invertebrate predation seems to be of relatively minor importance in controlling the population. While predatory invertebrates are present, they are never very abundant relative to the prey species. Vast numbers of small cladocerans, ostracods, and *S. exspinosus* are present during the rainy season, suggesting that the herbivores can reproduce themselves beyond the control of the predators. The persistence of the *Simocephalus* population to a few individuals in the last wet depressions in the ditch as it dries suggests that predation has little effect, even when numbers are low. If one compares the size of the field-collected individuals from Archer to the size of the laboratory-reared animals at day 14 and to the size of field-collected animals from the population subjected to heavy fish predation in Pine Pond, one sees that the Archer population contains quite large individuals in greater numbers than would be expected if predation were important. This information must be used with caution but does indicate that Archer individuals can and do escape predation long enough to grow to a large size on a regular basis while large individuals in the Pine populations are rare.

As the frequency of washouts decreases and finally stops, the population could reach carrying capacity, and the pond would no longer be supplied with new water rich in nutrients. Nutrients

would be depleted or put into the standing crop of plants unusable by *Simocephalus*, and competition for food would increase. As the pond is reduced in volume, crowding would become a more important D.D. mortality factor.

The data indicate that the Archer population did not show the expected changes in the population parameters commonly examined. One might expect that only one clone was present throughout the season, and that individuals should, therefore, not reflect any changes when reared under similar conditions at different times. Sexual activity, however, was observed through much of the season by the collection of males and sexual females. Evidence suggests that *Simocephalus* females are capable of fertilizing their own sexual eggs (Hebert 1980). Self-fertilization would further decrease the probability of the population being comprised of a single clone because recombination could occur without the presence of males. Some *S. exspinosus* and *S. vetulus* cultured during this study, although isolated since birth, produced both ephippia and parthenogenetic eggs.

In order to find a possible explanation for the failure of the population to contain different genotypes under different conditions as predicted by the model, a food study was conducted to determine whether *S. exspinosus* with high r values at high food levels had lower r values at low food levels than specimens with low r values at high food levels. This study showed that some clones had higher r values over all food ranges tested than did other clones.

The other parameters commonly examined did not show a tradeoff either. The high r clones consistently reproduced at an earlier age and had the flexibility to reproduce at increasingly smaller sizes as food concentrations were reduced. The high r clones had patterns of age-specific size and size-specific fecundity that allowed greater age-specific fecundity. The low r clone had no reproduction at the lowest food level and had higher death rates at the lower food levels than the high r clones. The high r clones showed greater flexibility to changing food levels, indicating that they could adapt better to a wide range of conditions. Since some genotypes were more successfull at all food levels than other genotypes, the successful genotypes would be more fit under most conditions, and, as seen in the previous experiment, a shift towards a lower $r_m$ with increased D.D. selection would not occur.

The size of young and eggs was seen to be consistent over the entire life of the parent except that young were sometimes smaller from the earliest reproductions. This rules out the possibility of the manipulation of egg and young size as a method for regulating the quality and quantity of offspring at various ages. *Simocephalus exspinosus* produced the largest eggs and young, followed by *S. serrulatus* and then by *S. vetulus*.

Numerous investigators have shown that planktonic invertebrates respond to visual and nonvisual predation in different ways. Several factors determine whether a certain predator can successfully catch and eat a certain prey item: size, body structure, and pigmentation (Confer and Blades 1975; Dodson 1970, 1972, 1974a,b; Hairston 1979a,b;

Kerfoot 1974, 1975, 1977a,b, 1978; Kerfoot and Peterson 1980; Mellors 1975; O'Brien and Vinyard 1978; O'Brien et al. 1979; Sprules 1972; Werner and Hall 1974; Zaret 1972a, b; Zaret and Kerfoot 1975).

Size-selective predation by visual predators favors small specimens. The visually-oriented vertebrate predators generally prefer prey greater than 1mm (Dodson 1974b) and would impose a limit on the maximum size to which a prey could be expected to grow. Individuals capable of reproducing at a size below that favored by the predators would have a great selective advantage over the larger forms.

Size-selective predation by nonvisual predators heavily favors large individuals. Invertebrates generally prefer prey less than 1mm (Dodson 1974b), being unable to handle larger individuals effectively. A prey animal could free itself from nonvisual predation by growing too large for the predator to eat. Invertebrate predation would favor those individuals capable of reaching a large size quickly.

Body structures may develop in a population in response to predation. Cyclomorphic cladoceran populations may contain individuals with elongated spines, expanded helmets, and other structures that would help make them more difficult for an invertebrate predator to handle (Dodson 1974b; Kerfoot 1975, 1977a, b, 1978; Kerfoot and Peterson 1980; O'Brien and Vinyard 1978; O'Brien et al 1979). These structures may serve as obstructions that do not allow the predator to manipulate the prey successfully after it had been captured. Structures cost the individual energy otherwise usable in

growth and reproduction, thereby reducing the rate of increase for that morph (Dodson 1974b; Kerfoot 1977b, 1975; Kerfoot and Peterson 1980; O'Brien and Vinyard 1978; Zaret 1972a, b). When visual predators remove most of the invertebrate predators these structures are not worth the cost, and forms without the structures would predominate due to greater reproductive ability.

Pigmentation is not influenced by nonvisual predation but promotes negative selection in planktonic populations subjected to visual predation and positive selection in some populations not subjected to visual predation. Planktonic individuals that are heavily pigmented, with the pigmentation in the body (Dodson 1974b; Hairston 1974a, b; Mellors 1975; O'Brien et al. 1979) or concentrated in the eyespot (Zaret 1972a; Zaret and Kerfoot 1975), are more conspicuous than cryptic clear individuals. Being conspicuous increases predation on and selection against pigmented morphs, allowing unpigmented forms to predominate. In the absence of visual predation, pigmentation may help protect against photodamage (Hairston 1979a, b).

Combining these factors into an overview one sees that planktonic populations subjected to visual predation tend to be composed of small individuals without heavy pigmentation and lacking elongate or expanded body structures while individuals in a population subjected to nonvisual predation are generally larger with elongated or expanded body features and heavier pigmentation.

*Simocephalus*, however, are not planktonic. They use a cervical gland to attach to the substrate and filter feed from a stationary position. Factors determining their resistance to predation are somewhat different from those of the planktonic forms.

The results show that as the importance of fish predation, as judged by the abundance of fish relative to the abundance of invertebrate predators, increased, the pigmentation in the shell, not the eyespot, became heavier. The best contrast is between Archer and Pine populations of *S. exspinosus*. Archer Pond is devoid of fish but has a few invertebrates capable of eating *S. exspinosus*, while Pine Pond has an abundance of fish and few invertebrates. Archer individuals showed no body pigmentation while Pine specimens were quite dark. The difference was significant. *Simocephalus vetulus* and *S. serrulatus* showed a similar response. A significant difference was seen between *S. serrulatus* from River Styx Bridge, a site with abundant fish, and those from Stock Pond, a site with few visual predators and abundant invertebrates. In *S. vetulus*, Psychology Pond had the lightest specimens. This site has no fish or abundant invertebrates. The darkest specimens came from Pine Pond, a site with abundant fish and few invertebrates. Specimens from Lake Alice, a lake with an abundance of both types of predators, were intermediate with regard to pigmentation.

Unlike planktonic cladocerans, the benthic *Simocephalus* would be at a disadvantage if they were not highly colored in a habitat containing numerous visual predators. *Simocephalus* most likely escape detection by hiding against a dark background rather than by being transparent. Their pigmentation, which is both light and dark, produces a mottled pattern that blends into the nonuniform substrate. A pattern of dark vertical stripes is often seen in all three species. This pattern is used by a host of other animals to blend with the background.

The animals used for the pigmentation study were collected from the field, not reared in the laboratory. Because of this, environmental factors may be cited as the reason for the dark coloration. Perhaps some of the color is environmentally induced, but not all. Specimens from the same sites were reared for many generations in the laboratory in white surroundings and still retained a considerable amount of color. The quantity of the pigmentation may be affected by the environment, but the existence of the pigmentation pattern is under genetic control. Two habitats, Mt. Vernon and Pine, were very similar to each other with the exception of the much greater abundance of fish in Pine. Both sites were shaded with highly stained water. Mt. Vernon individuals showed no pigmentation while Pine specimens did. If the pigmentation were caused by staining of the shell from chemicals in the water, one would expect the color to remain in the shell as it was cast off during a molt. This was not the case. The color remained in the animal, and the shed skin was clear. Also, if staining caused pigmentation, one would expect to see no pigmentation in the laboratory-reared animals.

In addition to pigmentation, other differences appeared between populations subjected to and not subjected to heavy fish predation. Two populations of *S. expinosus* lend themselves well to this comparison: Pine's population, subjected to heavy fish predation, and Archer's population, not subjected to visual predators. The most obvious difference is abundance. Pine's population was never as vast as Archer's. No attempt was made to determine the densities, but dips of the collecting pan in Pine Pond rarely produced more than one or

two specimens while a dip in Archer Pond often produced 50 or more. Fish predation in Pine Pond presumably kept the population quite small at all times. Another obvious difference was the size of field-collected individuals. Large animals were seen rarely in Pine Pond but were common in Archer. Heavy visual predation reduced the number of large individuals by size-selective removal. The comparison of the size of wild-caught animals to reared animals' sizes at day 14 for both habitats indicates that Pine individuals reached the larger, attainable sizes in the field less often than did Archer specimens. While differences in population size and the size of field-caught animals are not population parameters under genetic control, they do help illustrate the presence of predation, the effects of predation on the individual, and the importance of developing defenses against visual predators.

One of the defenses seen through laboratory rearings also deals with size. The Pine population contained specimens that did not grow as large. Archer individuals had significantly larger age-specific size than Pine specimens from birth through day 14. This size difference can also be seen in the growth rate figures, with Pine specimens reaching their asymptotic size more quickly. Despite producing smaller young, Pine specimens were not significantly different from Archer animals with regard to size-specific fecundity. This is probably due to a reduction in the brood chamber volume caused by the elongation and streamlining found in Pine specimens. The difference in age-specific size and lack of a difference in size-specific fecundity suggest a difference in age-specific fecundity.

Archer individuals generally had greater age-specific fecundity and, as a consequence, had greater $r_m$ values than Pine animals.

The relationship between eyespot size and visual predation for *Simocephalus* seems to follow the planktonic pattern. Eyespots of a population of *S. exspinosus* subjected to no visual predation (Archer) were significantly larger at all body ranges tested than eyespots of three populations of the same species from sites containing some visual predators (Mt. Vernon, Puddle, and Pine). No significant differences were evident among the eyespots from the three latter populations. The slope of the line produced by plotting $\log_{10}$ eyespot size against $\log_{10}$ body length was greater for the Archer population than for the other three populations, suggesting that eyespot size-selective predation is less intense in Archer Pond than in Mt. Vernon, Puddle, or Pine Ponds.

The three major morphological defenses against visual predation, eyespot size reduction, body size reduction, and increased pigmentation, seem to be selected independently of each other. Mount Vernon individuals have small eyespots, are unpigmented, but are quite large due to intense size-selective predation by invertebrates. Such a combination of features could occur if predation by a small and infrequent population of fish is not heavy enough to overshadow the intense nonvisual selective pressures of numerous invertebrates or to make an expenditure on body pigmentation energetically feasible, but is sufficient to alter the eyespot size.

Contrasting predator avoidance tactics of planktonic invertebrates with those of the benthic *Simocephalus*, one sees some similarities

but also some differences that are consistent with the different life style.

Both types of organisms respond to visual predation by a reduction in the size of the individuals in the population. Visually-oriented predators remove the larger individuals, causing selection for those forms that can mature and reproduce at a smaller size. In populations subjected to heavy nonvisual predation, animals grow to a large size very quickly, reducing the threat of predation by being too big for these predators to handle effectively.

Benthic *Simocephalus* do not show the development of expanded helmets or elongated spines when confronted with invertebrate predation. Their growth rate is most likely high enough to allow them to become too large too quickly for nonvisual predators. The morphs and species of *Simocephalus* with the most conspicuous spines or with the most expanded features are actually those subjected most heavily to visual predators.

Pigmentation is quite different between the groups. Heavy coloration of both light and dark patches provides camouflage against a dark and uneven substrate for *Simocephalus*. Heavy pigmentation in planktonic animals would make them more visible when suspended in the water. The role of pigmentation in protection against photodamage in *Simocephalus* was not investigated. Since egg-carrying females and potentially light-sensitive newborn normally inhabit the substrate, they are not as susceptible to photodamage as are zooplanktors. Thus in the absence of selective pressures by visually-oriented predators, the cost of pigmentation may surpass the benefit.

The ratio of eyespot size to body length is reduced by visual predation in both types of animals, is reduced significantly even by infrequent exposure to visually-oriented predation, and appears to undergo selection independent of the selection affecting body pigmentation.

Reproductive ability is greater for *Simocephalus* in forms not subjected to visual predation while it is greater in planktonic forms not subjected to heavy nonvisual predation. Planktonic animals must spend energy otherwise usable for reproduction on the production of spines or other additional body structures useful in protection against invertebrate predation while *Simocephalus* must expend energy on processes, such as pigment production, that are protection against visual predators.

The key characteristics of the three species of *Simocephalus* present in the area were examined to see if they were consistent in local populations. Three characteristics from Ward and Whipple (1959)--the shape of the ocellus, the presence of spinules on the vertex, and the type of spines on the postabdominal claw--were examined from field-collected specimens. The spination of the postabdominal claw proved to be the best character for positive identification. The postabdominal claw of *S. exspinosus* has a proximal pecten of long spines that are easily distinguishable from the smaller distal spines. *Simocephalus serrulatus* has heavy spines along the entire length of the claw while *S. vetulus* has very fine spines along the entire length. A compound microscope was used to examine the claws after their dissection from the animal. Although these spines were the

best character, they were difficult to see on live animals. The shape of the ocellus is most distinctive for *S. vetulus*, which has an irregular ocellus from which a line leads anteriorly. The other species do not have this line, although some *S. serrulatus* have a very long thin ocellus. The ocellus is very useful in identifying *S. vetulus* but is not always conclusive due to pigmentation or some other obstruction of the view of the ocellus. Likewise, the tuft of spinules on the vertex of *S. serrulatus* is not always conclusive. Some individuals do not show that character as well as others. The spinules, however, were never seen on the other species. *Simocephalus exspinosus* is the most rounded species, showing no sharp angles at the vertex or hinge. *Simocephalus serrulatus* has an elongate vertex with a sharp angle at the end and has a sharp point at the hinge, often with heavy spines on it. *Simocephalus vetulus* has an elongate but rounded vertex and a blunt point at the hinge. *Simocephalus vetulus*, and to a lesser extent *S. serrulatus*, has a vertically and posteriorly extended brood chamber that *S. exspinosus* does not have.

From the life history parameters and the types of habitats from which the species of *Simocephalus* were collected, some general comparisons of the ecology of the three species can be made. Considerable overlap exists, but certain trends are evident. The species tend to be found in different types of habitats. *Simocephalus exspinosus* is the predominant species in temporary ponds, *S. serrulatus* is found in permanent bodies of water, and *S. vetulus* can be found in both types of habitats, often in the presence of one of the other species. *Simocephalus exspinosus* was regularly collected from 6

sites, all temporary. One site, Pine, was filled with water during most of the study period but has been observed dry. In this site *S. vetulus* coexists with *S. exspinosus*. Both of these species were also found in Psychology Pond, but *S. vetulus* may have been recently introduced from Lake Alice by ecology classes. *Simocephalus exspinosus* was never collected from the same site as *S. serrulatus*. *Simocephalus serrulatus* was regularly collected from 4 sites, 3 of them permanent. In one site, Biven's Arms, *S. serrulatus* coexisted with *S. vetulus*. *S. vetulus* was regularly collected from 5 sites, 3 permanent and 2 temporary, and coexisted with *S. exspinosus* in 2 and *S. serrulatus* in one.

In temporary ponds ephippia production is necessary to maintain a population between dry spells. Male and sexually female *S. exspinosus* were seen frequently in the field and occasionally produced in the laboratory. Male and ephippia-bearing *S. vetulus* were observed but no evidence of sexual reproduction in *S. serrulatus* was ever observed in either the field or laboratory. This would imply that *S. serrulatus* is less likely to inhabit temporary ponds than the other species and that *S. exspinosus* can reestablish active populations in ephemeral ponds most easily of the three species.

Age-specific size was significantly different for most ages among the species, with *S. exspinosus* being the largest and *S. vetulus* the smallest. Growth rates show that *S. vetulus* reached its asymptotic value most quickly, followed by *S. serrulatus* and then by *S. exspinosus*. These results suggest that *S. exspinosus* would do well in temporary

ponds devoid of fish predation while *S. serrulatus* would be at an advantage when visual predation was heavy. The small size of *S. vetulus* is not well understood. Burns (1968) demonstrated that large cladocerans feed on larger food particles than do small cladocerans. Perhaps *S. vetulus* is capable of feeding on smaller food particles, thus reducing interspecific competition.

Size-specific fecundity was also significantly different among the species with *S. vetulus* having the greatest values and *S. exspinosus* the smallest. The small size of *S. vetulus* young allows more young to be packed into the brood chamber. In addition, this species develops an expanded brood chamber with the onset of reproduction so that the volume available for young is increased. *Simocephalus serrulatus* also shows this expansion to a degree.

Since the species with the largest age-specific size showed the smallest size-specific fecundity, the age-specific fecundity should have been similar for the three species. Very little difference was seen in the age-specific fecundity for the species. Likewise, there was no significant difference in $r_m$ among the species.

Age at first reproduction was significantly smaller for *S. serrulatus* than for the other species. This would be an advantage in ponds containing fish.

Size at first reproduction was significantly different among the species with *S. vetulus* being the smallest and *S. exspinosus* the largest.

Death rates through day 14 were somewhat higher for *S. exspinosus* than for the other species.

Clear interhabitat intraspecific comparisons can only be made for *S. exspinosus* with the present data. The selective pressures of predation were obviously different in several sites containing this species. Mount Vernon, Santa Fe, and Tennis Court Ponds were most highly affected by nonvisual predation although some visual predators may have been present at times. The effects of heavy visual predation by fish, salamanders, and visually-oriented insects were seen in Puddle and especially Pine. Very little predation of any sort was evident in Archer Pond. Differences in several life history parameters can be attributed to varying degrees of the opposing selective forces. Heavy nonvisual predation caused greater age-specific size, greater age-specific fecundity, and greater size at first reproduction in the first three sites. Heavy visual predation caused opposite trends in Puddle and Pine Ponds. The Archer population, practically unaffected by either selective force, generally had values between the two extremes.

The differences in the opposing selective forces of visual versus nonvisual predation were not as clear in sites from which the other two species were collected. Most sites contained both types of predators, and accurate measurements of the intensities of each type of selective force were not attempted. For this reason no attempt has been made to explain differences in life history parameters on the basis of varying selective forces on these two species. Pigmentation, however, appears to be affected only by visual predation, and increases in pigmentation have been associated with increased visual predation pressures because opposing selective forces due to nonvisual predation do not exist for this trait.

Table 1. Survival rate of 3 species of *Simocephalus* cladocerans to age 14 days.

| | *S. exspinosus* | *S. vetulus* | *S. serrulatus* |
|---|---|---|---|
| $\bar{X}$ | 0.91 | 0.82 | 0.90 |
| $s^2$ | 0.029 | 0.044 | 0.012 |
| Number of clones | 40 | 9 | 5 |

Table 2. Intrinsic rate of natural increase ($r_m$) for 3 species of *Simocephalus*.

| | *S. exspinosus* | *S. vetulus* | *S. serrulatus* |
|---|---|---|---|
| $\bar{X}$ | 0.619 | 0.612 | 0.417 |
| $s^2$ | 0.005 | 0.003 | 0.001 |
| Number of clones | 40 | 9 | 5 |

Table 3A. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. serrulatus* from the River Styx Pond.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.134-1.228 | 3.00 | 0 | 2 |
| 1.229-1.341 | 3.00 | -- | -- |
| 1.342-1.454 | 10.50 | 4.00 | 4 |
| 1.455-1.568 | 5.75 | 4.83 | 6 |
| 1.569-1.681 | 11.10 | 5.60 | 10 |
| 1.682-1.795 | 15.20 | 7.50 | 6 |
| 1.796-1.908 | 16.33 | 11.80 | 10 |
| 1.909-2.021 | 18.75 | 12.75 | 4 |
| 2.022-2.135 | 20.68 | 8.00 | 1 |
| 2.136-2.248 | 23.53 | 10.00 | 1 |
| 2.249-2.362 | 24.50 | -- | -- |
| 2.263-2.475 | 22.00 | -- | -- |

Table 3B. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. serrulatus* from Stock Pond.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.342-1.454 | 5.75 | -- | -- |
| 1.455-1.568 | 4.40 | 0 | 3 |
| 1.569-1.681 | 8.14 | 0 | 1 |
| 1.682-1.795 | 11.11 | 4.75 | 4 |
| 1.796-1.908 | 13.20 | 4.25 | 4 |
| 1.909-2.021 | 14.25 | 6.80 | 5 |
| 2.022-2.135 | 17.78 | 11.00 | 4 |
| 2.136-2.248 | 20.83 | 8.00 | 2 |
| 2.249-2.362 | -- | 14.00 | 2 |
| 2.363-2.475 | -- | 22.33 | 3 |
| 2.476-2.588 | -- | 26.60 | 5 |
| 2.589-2.702 | -- | 25.67 | 3 |
| 2.703-2.815 | -- | 32.50 | 2 |
| 2.816-2.929 | -- | 38.00 | 2 |

Table 3C. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. serrulatus* from River Styx Bridge.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.229-1.341 | -- | 0 | 2 |
| 1.342-1.454 | 3.00 | 4.00 | 5 |
| 1.455-1.568 | 7.13 | 5.00 | 4 |
| 1.569-1.681 | 8.50 | 5.00 | 5 |
| 1.682-1.795 | 14.43 | -- | -- |
| 1.796-1.908 | 16.27 | 8.00 | 3 |
| 1.909-2.021 | 19.60 | -- | -- |
| 2.022-2.135 | 19.78 | -- | -- |
| 2.136-2.248 | 17.06 | 11.00 | 1 |
| 2.249-2.362 | 17.00 | -- | -- |

Table 3D. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. vetulus* from Pine Pond.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.134-1.228 | -- | 5.00 | 3 |
| 1.229-1.341 | 5.00 | 6.00 | 1 |
| 1.342-1.454 | 6.75 | 7.00 | 6 |
| 1.455-1.568 | 7.00 | 12.88 | 9 |
| 1.569-1.681 | 12.85 | 14.50 | 8 |
| 1.682-1.795 | 13.52 | 17.43 | 7 |
| 1.796-1.908 | 14.11 | 21.40 | 5 |
| 1.909-2.021 | 17.38 | 25.00 | 3 |

Table 3E. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. vetulus* from Lake Alice.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.134-1.228 | 7.00 | 2.00 | 5 |
| 1.229-1.341 | 5.73 | 4.75 | 4 |
| 1.342-1.454 | 7.85 | 6.74 | 22 |
| 1.455-1.568 | 12.36 | 8.47 | 20 |
| 1.569-1.681 | 16.38 | 7.63 | 8 |
| 1.682-1.795 | 18.66 | 12.00 | 3 |
| 1.796-1.908 | 21.25 | -- | -- |
| 1.909-2.021 | 23.63 | -- | -- |

Table 3F. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. vetulus* from Psychology Pond.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.134-1.228 | 2.00 | 1.00 | 6 |
| 1.229-1.341 | 2.73 | 2.00 | 10 |
| 1.342-1.454 | 5.52 | 3.80 | 8 |
| 1.455-1.568 | 9.04 | 5.45 | 19 |
| 1.569-1.681 | 13.38 | 6.67 | 14 |
| 1.682-1.795 | 17.36 | 8.69 | 15 |
| 1.796-1.908 | 18.90 | 8.50 | 3 |
| 1.909-2.021 | 22.00 | -- | -- |

Table 3G. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. exspinosus* from Archer.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.342-1.454 | 5.00 | 0 | 2 |
| 1.455-1.568 | 4.75 | 0 | 6 |
| 1.569-1.681 | 8.60 | 4.00 | 12 |
| 1.682-1.795 | 9.60 | 4.40 | 9 |
| 1.796-1.908 | 12.55 | 5.76 | 17 |
| 1.909-2.021 | 14.42 | 7.50 | 14 |
| 2.022-2.135 | 15.61 | 7.62 | 22 |
| 2.136-2.248 | 16.35 | 8.22 | 20 |
| 2.249-2.362 | 18.08 | 9.17 | 12 |
| 2.363-2.475 | 20.60 | 10.38 | 10 |
| 2.476-2.588 | 27.00 | 20.00 | 1 |
| 2.589-2.702 | -- | 21.00 | 1 |
| 2.703-2.815 | -- | 30.43 | 7 |
| 2.816-2.929 | -- | 35.20 | 5 |
| 2.930-3.042 | -- | 28.50 | 2 |

Table 3H. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. exspinosus* from Pine Pond.

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.229-1.341 | 4.00 | -- | -- |
| 1.342-1.454 | 4.17 | 5.09 | 13 |
| 1.455-1.568 | 5.65 | 5.67 | 3 |
| 1.569-1.681 | 7.45 | 7.00 | 7 |
| 1.682-1.795 | 12.13 | 7.83 | 12 |
| 1.796-1.908 | 14.69 | 11.50 | 4 |
| 1.909-2.021 | 15.85 | 11.00 | 3 |
| 2.022-2.135 | 14.60 | 24.00 | 3 |
| 2.136-2.248 | 12.00 | 7.00 | 1 |
| 2.249-2.362 | 21.00 | -- | -- |
| 2.363-2.475 | 18.00 | 41.00 | 1 |
| 2.476-2.588 | 5.00 | -- | -- |

Table 3I. Comparison of size-specific fecundity of field-collected and laboratory-reared *S. exspinosus* from Puddle

| Length of adult (mm) | Mean number of young (reared) | Mean number of eggs (field) | Number of field-collected adults |
|---|---|---|---|
| 1.455-1.568 | 7.00 | 0 | 1 |
| 1.569-1.681 | 5.71 | 2.00 | 2 |
| 1.682-1.795 | 7.80 | 1.00 | 2 |
| 1.796-1.908 | 11.90 | 7.00 | 3 |
| 1.909-2.021 | 15.50 | 7.00 | 2 |
| 2.022-2.135 | 15.80 | 10.60 | 6 |
| 2.136-2.248 | 17.60 | 15.25 | 10 |
| 2.249-2.362 | 15.57 | 20.50 | 9 |
| 2.363-2.475 | 18.00 | 20.46 | 14 |
| 2.476-2.588 | 26.00 | 11.67 | 3 |
| 2.589-2.702 | -- | 19.50 | 2 |
| 2.703-2.815 | -- | 16.33 | 2 |
| 2.816-2.929 | -- | 18.33 | 3 |
| 2.930-3.042 | -- | 38.50 | 2 |
| 3.043-3.155 | -- | 29.67 | 3 |
| 3.156-3.269 | -- | 0 | 1 |

Table 4. Body length at age 14 days and $r_m$ values for January and April cohorts of the same clones of *Simocephalus*.

| Species | Date | $r_m$ | Body length (mm) |
|---|---|---|---|
| *S. exspinosus* | 25 January | 0.706 | 2.61 |
| | 13 April | 0.702 | 2.59 |
| *S. vetulus* | 20 January | 0.579 | 1.89 |
| | 14 April | 0.580 | 1.91 |

Table 5. $r_m$ values and analysis of variance of cloned Archer rearings. Number of generations.

Means:

| Date: | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
|---|---|---|---|---|---|---|
| Mean: | 0.657 | 0.627 | 0.605 | 0.607 | 0.570 | 0.670 |
| n: | 2 | 8 | 9 | 10 | 5 | 6 |

Analysis of variance:

f= 1.44

DF/df= 5/34

p= 0.2358

Estimate of mean generation time = 8 days

Estimate of the number of generations of *S. exspinosus* in the Archer site = 10 generations

Table 6. Size at first reproduction of cloned Archer rearings.

Means:

| Date: | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
|---|---|---|---|---|---|---|
| Mean (mm): | 1.975 | 1.838 | 1.847 | 1.826 | 1.799 | 2.006 |
| n: | 2 | 8 | 7 | 10 | 5 | 5 |

Analysis of variance:

| | |
|---|---|
| f= | 1.61 |
| DF/df= | 5/31 |
| p= | 0.1874 |

Table 7. Age of first reproduction of cloned Archer rearings,

Means:

| Date: | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
|---|---|---|---|---|---|---|
| Mean (days): | 4.00 | 3.88 | 4.33 | 4.30 | 3.80 | 4.17 |
| n: | 2 | 8 | 9 | 10 | 5 | 6 |

Analysis of variance:

| | |
|---|---|
| f= | 0.8200 |
| DF/df= | 34/4 |
| p= | 0.5425 |

Table 8. Size of newborn of cloned Archer rearings.

Means:

| Date: | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
|---|---|---|---|---|---|---|
| Mean (mm): | 0.803 | 0.770 | 0.756 | 0.743 | 0.756 | 0.745 |
| n: | 2 | 8 | 7 | 10 | 5 | 5 |

Analysis of variance:

| | |
|---|---|
| f= | 1.01 |
| DF/df= | 5/31 |
| p= | 0.4284 |

Table 9. Death rates (number of dead/number of days lived) of cloned Archer rearings through day 14.

| Date | Death Rate |
|---|---|
| Jan 15 | 0.0155, 0 |
| Jan 25 | 0.0233, 0.0155, 0, 0, 0, 0, 0, 0 |
| Feb 12 | 0.0229, 0.0240, 0.0072, 0.0182, 0, 0, 0, 0, 0, 0 |
| Feb 28 | 0.0164, 0.0092, 0, 0, 0, 0, 0, 0, 0, 0 |
| Mar 19 | 0.0930, 0.0816, 0.0825, 0.0164, 0.0632, 0.0612 |
| Mar 27 | 0, 0, 0, 0, 0 |

Table 10. Growth rates of cloned Archer rearings.

| Date | Growth Rate |
|---|---|
| Jan 15 | 0.718 |
| Jan 25 | 0.462 |
| Feb 12 | 0.560 |
| Feb 28 | 0.590 |
| Mar 19 | 0.584 |
| Mar 27 | 0.558 |

Table 11A. m(x) of cloned Archer rearings; means.

| Days | 15Jan | 25Jan | 12Feb | 28Feb | 19Mar | 27Mar |
|---|---|---|---|---|---|---|
| 3 | ---- | 1.85 | ---- | 5.00 | 1.11 | ---- |
| 4 | 7.35 | 5.58 | 4.60 | 5.04 | 4.93 | 7.90 |
| 5 | 6.25 | 3.65 | 6.20 | 7.40 | 6.69 | 4.92 |
| 6 | 10.60 | 8.95 | 8.88 | 8.13 | 4.27 | 17.44 |
| 7 | 10.28 | 5.52 | 9.45 | 6.78 | 3.00 | 7.13 |
| 8 | 16.00 | 12.67 | 9.77 | 2.68 | 6.01 | 26.20 |
| 9 | 18.72 | 7.23 | 6.40 | 7.96 | 8.52 | 14.76 |
| 10 | 2.55 | 12.82 | 6.24 | 4.91 | 14.25 | 20.68 |
| 11 | 12.05 | 7.38 | 7.65 | 9.29 | 3.90 | 7.05 |
| 12 | 4.45 | 13.90 | 8.13 | 5.46 | 5.79 | 21.38 |
| 13 | 12.92 | 7.63 | 11.23 | 10.14 | 11.75 | 8.56 |
| 14 | 4.92 | 13.57 | 7.41 | 5.65 | 10.63 | 18.10 |

Table 11B. m(x) of cloned Archer rearings; analysis of variance

| Day | DF/df | f | p | Duncan's Multiple Range Test |
|---|---|---|---|---|
| 3 | 2/2 | 8.35 | .1070 | |
| 4 | 24/5 | 0.55 | .7338 | |
| 5 | 5/30 | 1.02 | .4219 | |
| 6 | 5/31 | 4.62 | .0029 | Mar27 Jan15 Jan25 Feb12 Feb28 Mar19 |
| 7 | 5/26 | 1.24 | .3190 | |
| 8 | 5/28 | 25.44 | .0001 | Mar27 Jan15 Jan25 Feb12 Mar19 Feb28 |
| 9 | 5/30 | 2.09 | .0949 | |
| 10 | 5/28 | 9.71 | .0001 | Mar27 Mar19 Jan25 Feb12 Feb28 Jan15 |
| 11 | 5/25 | 1.40 | .2584 | |
| 12 | 5/29 | 14.49 | .0001 | Mar27 Jan25 Feb12 Mar19 Feb28 Jan15 |
| 13 | 28/5 | 0.57 | .7214 | |
| 14 | 5/29 | 6.78 | .0003 | Mar27 Jan25 Mar19 Feb12 Feb28 Jan15 |

Table 12A. Age-specific size of cloned Archer rearings; means in mm.

| Day | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
|---|---|---|---|---|---|---|
| 0 | 0.7182 | 0.7749 | 0.7560 | 0.7447 | 0.7466 | 0.7258 |
| 1 | 1.1529 | 1.0331 | 0.9639 | 0.9136 | ------ | ------ |
| 2 | ------ | 1.4364 | 1.3230 | 1.3608 | 1.3041 | 1.4440 |
| 3 | 1.8900 | 1.7388 | 1.7199 | 1.5751 | ------ | ------ |
| 4 | ------ | 1.7993 | 1.7766 | 1.9562 | 1.8617 | 1.9656 |
| 5 | 2.0601 | 2.0915 | 1.9940 | 1.7955 | ------ | ------ |
| 6 | ------ | 2.0261 | 2.0412 | 2.0885 | 1.9467 | 2.2151 |
| 7 | 2.2302 | 2.2680 | 2.1924 | 1.9531 | ------ | ------ |
| 8 | ----- | 2.1848 | 2.2049 | 2.1357 | 2.0412 | 2.3965 |
| 9 | 2.3436 | 2.3814 | 2.2208 | 2.0726 | ------ | ------ |
| 10 | ------ | 2.3587 | 2.3814 | 2.2302 | 2.1735 | 2.5024 |
| 11 | 2.4381 | 2.4948 | 2.2964 | 2.3058 | ------ | ------ |
| 12 | ------ | 2.4268 | 2.4317 | 2.3720 | 2.2491 | 2.6233 |
| 13 | 2.4570 | 2.5704 | 2.3720 | 2.3814 | ------ | ------ |
| 14 | 2.6082 | 2.4948 | 2.4948 | 2.4381 | 2.3058 | 2.6989 |

Table 12B. Age-specific size of cloned Archer rearings; analysis of variance.

| Day | DF/df | f | p | Duncan's Multiple Range Test |
|---|---|---|---|---|
| 0 | 5/30 | 1.17 | .3462 | |
| 1 | 3/11 | 3.90 | .0403 | |
| 2 | 16/4 | 0.91 | .4792 | |
| 3 | 3/11 | 2.53 | .1108 | |
| 4 | 4/16 | 2.37 | .0965 | |
| 5 | 3/11 | 6.59 | .0082 | 25Jan 15Jan 12Feb 28Feb |
| 6 | 4/16 | 4.56 | .0119 | 27Mar 28Feb 12Feb 25Jan 19Mar |
| 7 | 3/11 | 17.27 | .0002 | 25Jan 15Jan 12Feb 28Feb |
| 8 | 4/16 | 14.15 | .0001 | 27Mar 12Feb 25Jan 28Feb 19Mar |
| 9 | 3/11 | 18.14 | .0001 | 25Jan 15Jan 12Feb 28Feb |
| 10 | 4/16 | 8.96 | .0005 | 27Mar 12Feb 25Jan 28Feb 19Mar |
| 11 | 3/11 | 11.09 | .0012 | 25Jan 15Jan 28Feb 12Feb |
| 12 | 4/16 | 11.25 | .0002 | 27Mar 12Feb 25Jan 28Feb 19Mar |
| 13 | 3/11 | 8.45 | .0034 | 25Jan 15Jan 28Feb 12Feb |
| 14 | 5/15 | 16.37 | .0001 | 27Mar 15Jan 12Feb 25Jan 28Feb 19Mar |

Table 13. Size of eggs as a function of age of parents.

| Day | n | Mean (mm) | DF/df | f | p | Duncan |
|---|---|---|---|---|---|---|
| Austin Carey *S. vetulus* | | | | | | |
| 3 | 22 | .1986 | 3/140 | 6.70 | .0004 | 25 3 8 14 |
| 8 | 35 | .1963 | | | | |
| 14 | 37 | .1954 | | | | |
| 25 | 50 | .2076 | | | | |
| Biven's Arm *S. serrulatus* | | | | | | |
| 4 | 7 | .2116 | 3/42 | 12.61 | .0001 | 4 25 5 10 |
| 5 | 7 | .2076 | | | | |
| 10 | 11 | .1965 | | | | |
| 25 | 21 | .2081 | | | | |
| Biven's Arm *S. vetulus* | | | | | | |
| 4 | 12 | .1948 | 3/50 | 1.93 | .1375 | |
| 10 | 9 | .2024 | | | | |
| 15 | 10 | .2052 | | | | |
| 25 | 23 | .1972 | | | | |
| Mt. Vernon *S. exspinosus* | | | | | | |
| 3 | 11 | .2375 | 4/47 | 45.84 | .0001 | 13 9 3 25 19 |
| 8 | 11 | .2484 | | | | |
| 13 | 9 | .2494 | | | | |
| 19 | 10 | .2153 | | | | |
| 25 | 11 | .2175 | | | | |
| River Styx Pond *S. serrulatus* | | | | | | |
| 6 | 41 | .1990 | 100/2 | 0.38 | .6842 | |
| 11 | 28 | .2001 | | | | |
| 17 | 34 | .2013 | | | | |

Table 14A. Size of young born to parents of various ages in *S. exspinosus* collected from Mt. Vernon Pond.

| Day | n | Mean (mm) |
|---|---|---|
| 4-5-6 | 28 | 0.6872 |
| 7-8-9 | 10 | 0.7106 |
| 10-11-12 | 10 | 0.6804 |
| 13-14-15 | 10 | 0.7182 |
| 16-17-18 | 20 | 0.7182 |
| 19-20-21 | 21 | 0.7235 |
| 33 | 5 | 0.7182 |

| Analysis of variance | df | f | p |
|---|---|---|---|
| | 6/97 | 10.61 | .0001 |

Duncan: 19-20-21 33 13-14-15 16-17-18 7-8-9 4-5-6 10-11-12

Table 14B. Size of young born to parents of various ages in *S. vetulus* collected from Austin Carey Pond.

| Day | n | Mean (mm) |
|---|---|---|
| 3-4 | 37 | 0.5129 |
| 5-6 | 16 | 0.5436 |
| 7-8 | 51 | 0.5761 |
| 9-10 | 56 | 0.5655 |
| 11-12 | 40 | 0.5538 |
| 13-14 | 16 | 0.5625 |
| 15-16 | 37 | 0.5681 |
| 17-18 | 38 | 0.5689 |
| 19-20 | 45 | 0.5685 |
| 21-22 | 50 | 0.5708 |
| 23-24 | 31 | 0.5708 |

| Analysis of variance: | df | f | p |
|---|---|---|---|
| | 10/406 | 29.61 | .0001 |

Duncan: 7-8 21-22 23-24 17-18 19-20 15-16 9-10 13-14 11-12 5-6 3-4

Table 14C. Size of young born to parents of various ages in *S. vetulus* collected from Biven's Arm.

| Day | n | Mean (mm) |
|---|---|---|
| 3-4-5 | 34 | 0.5337 |
| 6-7-8 | 21 | 0.5761 |
| 9-10-11 | 28 | 0.5670 |
| 12-13-14 | 10 | 0.5760 |
| 15-16-17-18 | 24 | 0.5760 |
| 20-22-23 | 25 | 0.5760 |

| Analysis of variance: | df | f | p |
|---|---|---|---|
| | 5/136 | 9.68 | .0001 |

Duncan: 6-7-8 9-10-11 12-13-14 20-22-23 15-16-17 3-4-5

Table 14D. Size of young born to parents of various ages in *S. serrulatus* collected from Biven's Arm.

| Day | n | Mean (mm) |
|---|---|---|
| 4-5 | 25 | 0.5776 |
| 6-7 | 39 | 0.5893 |
| 8-9 | 25 | 0.5957 |
| 10-11 | 15 | 0.5923 |
| 12-13 | 15 | 0.6048 |
| 14-15 | 22 | 0.6101 |
| 16-17 | 25 | 0.5972 |
| 18-19 | 25 | 0.5972 |
| 20-21 | 25 | 0.5972 |

Analysis of variance:

| df | f | p |
|---|---|---|
| 8/207 | 2.43 | .0156 |

Duncan: 14-15 12-13 16-17 18-19 20-21 8-9 10-11 6-7 4-5

Table 14E. Size of young born to parents of various ages in *S. serrulatus* collected from River Styx Pond.

| Day | n | Mean (mm) |
|---|---|---|
| 3-4 | 63 | 0.6010 |
| 5-6 | 49 | 0.6294 |
| 7-8 | 50 | 0.6313 |
| 9-10 | 30 | 0.6301 |
| 11-12 | 45 | 0.6301 |
| 13-14 | 55 | 0.6188 |
| 15-16 | 39 | 0.6377 |

| Analysis of variance: | df | f | p |
|---|---|---|---|
| | 6/324 | 15.21 | .0001 |

Duncan: 15-16 13-14 7-8 9-10 11-12 5-6 3-4

Table 15. Relationship between food level and r of 3 different lines of *S. exspinosus*.
A. r values of the *S. exspinosus* food rearings.
B. Characteristics of plots of r-$\log_{10}$ food level.
C. Analysis of covariance of lines in "B".

| A. Food (cells/ml) | A | B | C |
|---|---|---|---|
| 1,000,000 | .568 | .550 | .473 |
| 500,000 | .547 | .527 | .450 |
| 250,000 | .466 | .448 | .407 |
| 50,000 | .368 | .401 | .204 |
| 5,000 | .204 | .286 | .002 |
| 0 | .019 | .086 | ---- |

| B. Clone | Slope | y intercept | x intercept | Correlation |
|---|---|---|---|---|
| A | .092 | -0.027 | 0.299 | .96 |
| B | .075 | 0.062 | -0.827 | .98 |
| C | .209 | -0.753 | 3.61 | .99 |

| C. | A/B | A/C | B/C |
|---|---|---|---|
| slope; p= | .3346 | .0090 | .0003 |
| y intercept; p= | .5726 | .1810 | 0.135 |

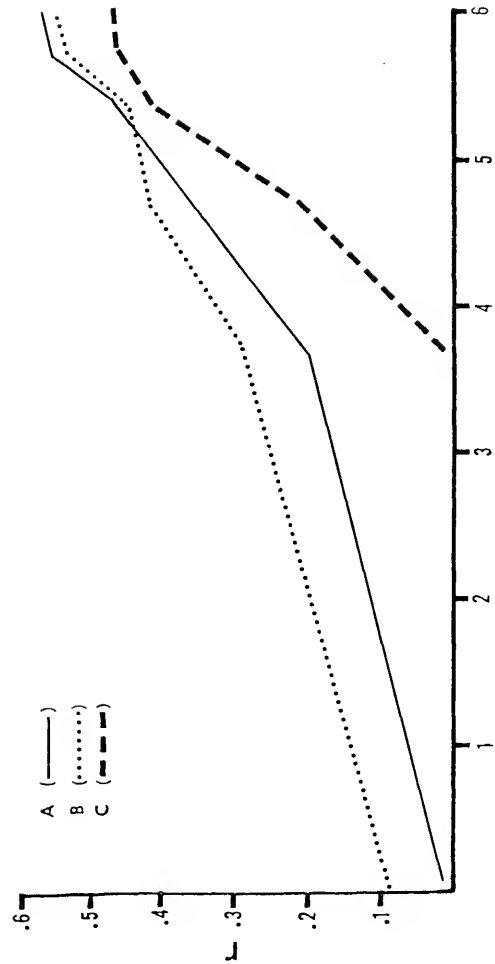


FIGURE 1: Relationship between food level and r of 3 different lines of *S. exspinosus*.

Table 16A. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 1,000,000 cells/ml.

| mm | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 1.229-1.341 | ---- | 5.00 | ---- | | |
| 1.342-1.454 | ---- | 6.67 | ---- | | |
| 1.455-1.568 | ---- | 8.25 | 3.33 | .0006 | |
| 1.569-1.681 | 6.00 | 10.17 | 5.50 | .0023 | B A C |
| 1.682-1.795 | 8.00 | 10.67 | 9.60 | .4830 | |
| 1.796-1.908 | 9.67 | 15.20 | 13.67 | .3767 | |
| 1.909-2.021 | 15.40 | 18.33 | 13.33 | .1100 | |
| 2.022-2.135 | 10.50 | 23.80 | 14.29 | .0035 | B C A |
| 2.136-2.248 | 17.00 | 31.00 | 16.83 | .0002 | B A C |
| 2.249-2.362 | 21.00 | ---- | 19.40 | .1652 | |
| 2.363-2.475 | 19.36 | ---- | ---- | | |
| 2.476-2.588 | 19.00 | ---- | ---- | | |

Table 16B. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 500,000 cells/ml.

| mm | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 1.229-1.341 | ---- | 8.00 | ---- | | |
| 1.342-1.454 | ---- | 6.00 | ---- | | |
| 1.455-1.568 | 4.00 | 9.17 | 4.00 | .0139 | B A C |
| 1.569-1.681 | 5.25 | 9.33 | 5.00 | .0001 | B A C |
| 1.682-1.795 | 9.33 | 13.57 | 10.00 | .1109 | |
| 1.796-1.908 | 14.50 | 17.11 | 14.25 | .0695 | |
| 1.909-2.021 | 17.50 | 19.50 | 14.20 | .0913 | |
| 2.022-2.135 | 20.83 | ---- | 15.33 | .0004 | |
| 2.136-2.248 | 20.57 | ---- | 17.00 | .0024 | |
| 2.249-2.362 | 19.00 | ---- | 17.00 | .2026 | |
| 2.363-2.475 | 21.50 | ---- | ---- | | |

Table 16C. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 250,000 cells/ml.

| mm | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 1.342-1.454 | ---- | 4.33 | ---- | | |
| 1.455-1.568 | 4.00 | 6.44 | 4.00 | .0661 | |
| 1.569-1.681 | 6.00 | 8.83 | 4.00 | .0027 | B A C |
| 1.682-1.795 | 10.50 | 10.78 | 6.83 | .0015 | B A C |
| 1.796-1.908 | 8.67 | 14.60 | 6.25 | .0055 | B A C |
| 1.909-2.021 | 10.29 | 15.20 | 11.00 | .0094 | B C A |
| 2.022-2.135 | 10.44 | ---- | 10.60 | .9421 | |
| 2.136-2.248 | 10.00 | ---- | 7.67 | .5938 | |

Table 16D. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 50,000 cells/ml.

| mm | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 1.229-1.341 | ---- | 3.25 | ---- | | |
| 1.342-1.454 | 2.00 | 4.71 | 1.00 | .0012 | B A C |
| 1.455-1.568 | 3.33 | 6.20 | 2.00 | .0001 | B A C |
| 1.569-1.681 | 5.67 | 6.30 | 2.75 | .0124 | B A C |
| 1.682-1.795 | 6.80 | 7.00 | 3.25 | .0408 | B A C |
| 1.796-1.908 | 9.00 | ---- | 3.50 | .0041 | |
| 1.909-2.021 | 9.83 | ---- | 3.00 | .0077 | |
| 2.022-2.135 | 10.67 | ---- | | | |

Table 16E. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 5,000 cells/ml.

| mm | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 1.229-1.341 | --- | 2.50 | ---- | | |
| 1.342-1.454 | 1.75 | 3.71 | ---- | .0013 | |
| 1.455-1.568 | 2.33 | ---- | 4.75 | .0009 | |
| 1.569-1.681 | 3.00 | 4.67 | 5.00 | .0041 | C B A |
| 1.682-1.795 | 3.00 | ---- | ---- | | |
| 1.796-1.908 | 4.50 | ---- | 5.00 | .6667 | |

Table 16F. Size-specific fecundity of 3 lines of *S. exspinosus* at a food level of 0 cells/ml.

| mm | A | B | C | p |
|---|---|---|---|---|
| 1.229-1.341 | ---- | 1.40 | ---- | |
| 1.342-1.454 | 1.25 | 3.00 | ---- | .0106 |
| 1.455-1.568 | 1.33 | 2.50 | ---- | .1328 |
| 1.569-1.681 | 1.00 | ---- | ---- | |

Table 17A. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 1,000,000 cells/ml.

| Day | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 4 | 6.80 | ---- | ---- | | |
| 5 | 11.17 | 8.17 | 3.25 | .0415 | A B C |
| 6 | 15.50 | 7.50 | 8.33 | .0174 | A C B |
| 7 | 16.00 | 9.40 | 11.40 | .0054 | A C B |
| 8 | 15.00 | 15.33 | 13.50 | .8822 | |
| 9 | 20.00 | 16.33 | 12.75 | .1165 | |
| 10 | 18.33 | 20.17 | 16.67 | .8009 | |
| 11 | 19.60 | 19.33 | 15.80 | .0439 | A B C |
| 12 | 19.33 | 22.60 | 21.00 | .7279 | |
| 13 | 19.40 | 15.67 | 15.60 | .1501 | |
| 14 | 19.00 | 16.60 | 18.00 | .9105 | |

Table 17B. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 500,000 cells/ml.

| Day | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 4 | 5.25 | ---- | ---- | | |
| 5 | 4.50 | 8.29 | 3.50 | .0018 | B A C |
| 6 | 10.00 | 8.00 | 9.00 | .7643 | |
| 7 | 15.33 | 11.80 | 9.17 | .1869 | |
| 8 | 18.17 | 9.33 | 17.00 | .0082 | A C B |
| 9 | 19.50 | 13.67 | 13.83 | .0957 | |
| 10 | 21.20 | 16.00 | 17.50 | .0279 | A C B |
| 11 | 20.67 | ---- | 13.67 | .0043 | |
| 12 | 20.60 | 12.67 | 18.00 | .0598 | |
| 13 | 21.00 | 20.00 | 16.00 | .1427 | |
| 14 | 16.67 | 17.67 | 16.50 | .9129 | |

Table 17C. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 250,000 cells/ml.

| Day | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 4 | 5.50 | ---- | ---- | | |
| 5 | 4.33 | 6.25 | 8.75 | .0001 | C B A |
| 6 | 8.50 | 5.33 | ---- | .0432 | |
| 7 | 9.17 | 9.00 | 4.50 | .0442 | A B C |
| 8 | 10.50 | 7.50 | 12.50 | .0753 | |
| 9 | 12.67 | 9.67 | 6.00 | .0768 | |
| 10 | 8.25 | 11.67 | 12.67 | .3685 | |
| 11 | 10.00 | 14.00 | 5.00 | .0040 | B A C |
| 12 | 10.00 | 7.67 | 7.00 | .4490 | |
| 13 | 12.67 | 13.67 | 7.67 | .0739 | |
| 14 | 8.00 | 10.00 | 5.00 | .5224 | |

Table 17D. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 50,000 cells/ml.

| Day | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 5 | 4.50 | 4.00 | ---- | .5908 | |
| 6 | 2.75 | 4.50 | 3.00 | .1239 | |
| 7 | 6.50 | 7.00 | 3.00 | .2866 | |
| 8 | 5.33 | 6.50 | 2.67 | .2470 | |
| 9 | 9.00 | 6.00 | 2.50 | .1484 | |
| 10 | 7.17 | 6.00 | 4.00 | .3241 | |
| 11 | 10.00 | 6.20 | ---- | .0188 | |
| 12 | 8.00 | 5.50 | 2.67 | .0983 | |
| 13 | 12.00 | 6.80 | 3.00 | .0117 | A B C |
| 14 | 7.00 | 4.50 | 2.67 | .0501 | |

Table 17E. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 5,000 cells/ml.

| Day | A | B | C | p | Duncan |
|---|---|---|---|---|---|
| 4 | ---- | 4.00 | ---- | | |
| 6 | ---- | 2.25 | ---- | | |
| 7 | 2.50 | 4.50 | ---- | .3333 | |
| 8 | 2.00 | 4.00 | 5.00 | .0029 | C B A |
| 9 | 3.00 | 4.67 | ---- | .0068 | |
| 10 | 2.00 | 4.00 | ---- | .0748 | |
| 11 | 2.75 | 4.00 | ---- | .4397 | |
| 12 | 2.00 | 5.00 | 5.00 | .0000 | B C A |
| 13 | 4.00 | 4.00 | ---- | 1.00 | |
| 14 | 3.00 | 5.00 | ---- | .0000 | |

Table 17F. Age-specific fecundity of 3 lines of *S. exspinosus* at a food level of 0 cells/ml.

| Day | A | B | C |
|---|---|---|---|
| 8 | ---- | 1.67 | ---- |
| 10 | ---- | 2.33 | ---- |
| 11 | 1.25 | ---- | ---- |
| 12 | ---- | 2.33 | ---- |
| 13 | 1.25 | ---- | ---- |
| 14 | ---- | 2.50 | ---- |

Table 18A. Age-specific size of 3 lines of *S. exspinosus* at a food level of 1,000,000 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7798 | 0.7371 | 0.7371 | .0015 | A B C |
| 1 | 1.0020 | 0.8316 | 0.8222 | .0001 | A B C |
| 2 | 1.3041 | 1.0350 | 1.0301 | .0001 | A B C |
| 3 | 1.6020 | 1.2712 | 1.2145 | .0001 | A B C |
| 4 | 1.6776 | 1.4791 | 1.4270 | .0009 | A B C |
| 5 | 1.8806 | 1.5026 | 1.5075 | .0001 | A C B |
| 6 | 2.0461 | 1.6303 | 1.7815 | .0001 | A C B |
| 7 | 2.1406 | 1.7059 | 1.8099 | .0001 | A C B |
| 8 | 2.2019 | 1.7577 | 1.9373 | .0001 | A C B |
| 9 | 2.2729 | 1.8617 | 2.0223 | .0001 | A C B |
| 10 | 2.3202 | 1.8995 | 2.1168 | .0001 | A C B |
| 11 | 2.3531 | 1.9656 | 2.1735 | .0001 | A C B |
| 12 | 2.4098 | 1.9800 | 2.2302 | .0001 | A C B |
| 13 | 2.4336 | 1.9940 | 2.2351 | .0001 | A C B |
| 14 | 2.4619 | 1.9989 | 2.2869 | .0001 | A C B |

Table 18B. Age-specific size of 3 lines of *S. exspinosus* at a food level of 500,000 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7844 | 0.7420 | 0.7371 | .0001 | A B C |
| 1 | 0.9828 | 0.8316 | 0.8554 | .0013 | A C B |
| 2 | 1.2569 | 1.0017 | 0.9972 | .0002 | A B C |
| 3 | 1.4270 | 1.2002 | 1.1718 | .0021 | A B C |
| 4 | 1.5736 | 1.3986 | 1.4081 | .0168 | A C B |
| 5 | 1.7343 | 1.4697 | 1.5264 | .0001 | A C B |
| 6 | 1.8004 | 1.5264 | 1.7248 | .0002 | A C B |
| 7 | 1.9138 | 1.6349 | 1.7861 | .0006 | A C B |
| 8 | 1.9989 | 1.7343 | 1.9327 | .0011 | A C B |
| 9 | 2.0745 | 1.7672 | 1.9656 | .0002 | A C B |
| 10 | 2.1312 | 1.8193 | 2.0737 | .0001 | A C B |
| 11 | 2.1973 | 1.8144 | 2.0934 | .0001 | A C B |
| 12 | 2.2208 | 1.8575 | 2.1641 | .0001 | A C B |
| 13 | 2.2732 | 1.8632 | 2.1784 | .0001 | A C B |
| 14 | 2.3274 | 1.9429 | 2.2162 | .0001 | A C B |

Table 18C. Age-specific size of 3 lines of *S. exspinosus* at a food level of 250,000 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7609 | 0.7326 | 0.7277 | .0227 | A B C |
| 1 | 0.8883 | 0.8127 | 0.9121 | .0244 | C A B |
| 2 | 1.0679 | 0.9545 | 1.0679 | .2636 | |
| 3 | 1.3136 | 1.1718 | 1.2947 | .4249 | |
| 4 | 1.5120 | 1.3657 | 1.4175 | .4760 | |
| 5 | 1.5642 | 1.4319 | 1.5264 | .4296 | |
| 6 | 1.7154 | 1.4931 | 1.6681 | .1382 | |
| 7 | 1.7626 | 1.5736 | 1.7343 | .1856 | |
| 8 | 1.8477 | 1.6303 | 1.8382 | .0108 | A C B |
| 9 | 1.8806 | 1.6587 | 1.8617 | .0207 | A C B |
| 10 | 1.9373 | 1.7437 | 1.9232 | .0170 | A C B |
| 11 | 2.0083 | 1.7672 | 1.9656 | .0093 | A C B |
| 12 | 2.0412 | 1.8050 | 1.9989 | .0074 | A C B |
| 13 | 2.0900 | 1.8333 | 2.0412 | .0012 | A C B |
| 14 | 2.1232 | 1.9278 | 2.0790 | .0189 | A C B |

Table 18D. Age-specific size of 3 lines of *S. exspinosus* at a food level of 50,000 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7609 | 0.7420 | 0.7277 | .0632 | |
| 1 | 0.8176 | 0.7749 | 0.8978 | .0001 | C A B |
| 2 | 0.9734 | 0.9639 | 1.0444 | .2838 | |
| 3 | 1.2334 | 1.2096 | 1.2240 | .9710 | |
| 4 | 1.3419 | 1.3563 | 1.3041 | .8291 | |
| 5 | 1.4837 | 1.3797 | 1.4508 | .4187 | |
| 6 | 1.5593 | 1.4364 | 1.4742 | .3832 | |
| 7 | 1.6378 | 1.5075 | 1.5687 | .2799 | |
| 8 | 1.6687 | 1.5547 | 1.6364 | .3508 | |
| 9 | 1.7388 | 1.5642 | 1.7074 | .0552 | |
| 10 | 1.7627 | 1.6114 | 1.7199 | .1284 | |
| 11 | 1.8382 | 1.6254 | 1.7702 | .0112 | A C B |
| 12 | 1.8522 | 1.6522 | 1.7891 | .0510 | |
| 13 | 1.9115 | 1.6685 | 1.8144 | .0049 | A C B |
| 14 | 1.9214 | 1.7120 | 1.8144 | .0288 | A C B |

Table 18E. Age-specific size of 3 lines of *S. exspinosus* at a food level of 5,000 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7655 | 0.7560 | 0.7277 | .0161 | A B C |
| 1 | 0.8082 | 0.7844 | 0.8460 | .1354 | |
| 2 | 0.9545 | 0.9545 | 0.9121 | .2082 | |
| 3 | 1.0868 | 1.1624 | 1.0747 | .2217 | |
| 4 | 1.2051 | 1.2474 | 1.2474 | .8673 | |
| 5 | 1.2663 | 1.3393 | 1.3608 | .3682 | |
| 6 | 1.3608 | 1.3771 | 1.4617 | .3480 | |
| 7 | 1.3846 | 1.4050 | 1.4617 | .5191 | |
| 8 | 1.4980 | 1.4300 | 1.4648 | .4608 | |
| 9 | 1.5358 | 1.4678 | 1.5120 | .6092 | |
| 10 | 1.5687 | 1.4867 | 1.5373 | .4462 | |
| 11 | 1.6039 | 1.5373 | 1.5876 | .7051 | |
| 12 | 1.6632 | 1.5623 | 1.6129 | .6031 | |
| 13 | 1.6946 | 1.5751 | 1.6507 | .3738 | |
| 14 | 1.7263 | 1.6129 | 1.6632 | .4437 | |

Table 18F. Age-specific size of 3 lines of *S. exspinosus* at a food level of 0 cells/ml.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| Day | A | B | C | p | Duncan |
| 0 | 0.7609 | 0.7560 | 0.7231 | .0066 | A B C |
| 1 | 0.8600 | 0.7704 | 0.8127 | .0764 | |
| 2 | 0.9499 | 0.8978 | 0.8743 | .0620 | |
| 3 | 0.9828 | 0.9972 | 0.9775 | .9311 | |
| 4 | 1.0444 | 1.0637 | 1.1529 | .3298 | |
| 5 | 1.0822 | 1.1340 | 1.2550 | .0642 | |
| 6 | 1.1484 | 1.1465 | 1.3325 | .0005 | C A B |
| 7 | 1.1484 | 1.2020 | 1.3514 | .0047 | C B A |
| 8 | 1.2474 | 1.3041 | 1.4553 | .0363 | C B A |
| 9 | 1.3325 | 1.3608 | 1.1843 | .7989 | |
| 10 | 1.4081 | 1.3608 | ------ | .1540 | |
| 11 | 1.4081 | 1.3986 | ------ | .8144 | |
| 12 | 1.5309 | 1.3986 | ------ | .0272 | |
| 13 | 1.5309 | 1.4364 | ------ | .1540 | |
| 14 | 1.5498 | 1.4931 | ------ | .3453 | |

Table 19. Relationship between food level and size at first reproduction of 3 lines of *S. exspinosus*.

| | Means (mm) | | | | |
|---|---|---|---|---|---|
| cells/ml | A | B | C | p | Duncan |
| 1,000,000 | 1.7154 | 1.5026 | 1.6303 | .0047 | A C B |
| 500,000 | 1.6443 | 1.4697 | 1.6443 | .0016 | A C B |
| 250,000 | 1.6020 | 1.4553 | 1.6870 | .0001 | C A B |
| 50,000 | 1.5075 | 1.3797 | 1.5940 | .0002 | C A B |
| 5,000 | 1.4791 | 1.3608 | 1.6254 | .0046 | C A B |
| 0 | 1.4081 | 1.2852 | ------ | .0073 | |

Table 20. Relationship between food level and age at first reproduction of 3 lines of *S. exspinosus*.

| | Means (days) | | | | |
|---|---|---|---|---|---|
| cells/ml | A | B | C | p | Duncan |
| 1,000,000 | 4.38 | 5.25 | 5.63 | .0011 | C B A |
| 500,000 | 4.88 | 5.13 | 6.25 | .0092 | C B A |
| 250,000 | 5.50 | 5.88 | 6.50 | .4160 | |
| 50,000 | 6.13 | 5.63 | 7.17 | .0174 | C A B |
| 5,000 | 7.88 | 5.86 | 8.00 | .0002 | C A B |
| 0 | 11.00 | 8.00 | ---- | .0000 | |

Table 21. A. Relationship between food level and growth rates of 3 lines of *S. exspinosus*.
B. Growth rates of cloned Archer rearings of *S. exspinosus*.
C. Growth rates of 3 species of *Simocephalus*
D. Growth rates of *S. exspinosus* from Archer and Pine Pond sites.

| A. Habitat | Food level (cells/ml) | | | | | |
|---|---|---|---|---|---|---|
| | 1,000,000 | 500,000 | 250,000 | 50,000 | 5,000 | 0 |
| A. | .607 | .478 | .370 | .421 | .301 | .331 |
| B. | .582 | .548 | .498 | .549 | .489 | .310 |
| C. | .553 | .605 | .465 | .401 | .443 | .395 |

| B. | Date of collection | | | | | |
|---|---|---|---|---|---|---|
| | Jan 15 | Jan 25 | Feb 12 | Feb 28 | Mar 19 | Mar 27 |
| | .718 | .462 | .560 | .590 | .584 | .558 |

| C. | Species | | |
|---|---|---|---|
| | *S. exspinosus* | *S. vetulus* | *S. serrulatus* |
| | .627 | .794 | .670 |

| D. | Collection site | |
|---|---|---|
| | Archer | Pine Pond |
| | .592 | .775 |

Table 22. Relationship between food level and death rate (number dead/number of days lived) of 3 lines of *S. exspinosus*.

| Food | A | B | C |
|---|---|---|---|
| 1,000,000 | 0.00 | 0.00 | 0.00 |
| 500,000 | .009 | .019 | 0.00 |
| 250,000 | .018 | .009 | .009 |
| 50,000 | .019 | .009 | .020 |
| 5,000 | .019 | .061 | .071 |
| 0 | .047 | .083 | .174 |

Table 23. Comparison of life history features of Pine Pond and Archer *S. exspinosus* populations.

| Parameters | Pine | Archer | P |
|---|---|---|---|
| $r_m$ | 0.566 | 0.645 | -- |
| size at first reproduction (mm) | 1.512 | 1.657 | >.05 |
| age at first reproduction (days) | 4.69 | 4.33 | >.05 |
| growth rate | 0.775 | 0.592 | -- |

Table 24. Age-specific size of Archer and Pine *S. exspinosus* populations. $P < .05$ at all ages.

| Day | Pine (mm) | Archer (mm) |
|---|---|---|
| 0 | 0.6324 | 0.7216 |
| 1 | 0.8476 | 0.9597 |
| 2 | 1.1098 | 1.3117 |
| 3 | 1.3695 | 1.5766 |
| 4 | 1.5309 | 1.7842 |
| 5 | 1.5819 | 1.8764 |
| 6 | 1.6965 | 1.9996 |
| 7 | 1.7316 | 2.0567 |
| 8 | 1.8144 | 2.1353 |
| 9 | 1.9051 | 2.1659 |
| 10 | 1.9187 | 2.2532 |
| 11 | 1.9565 | 2.2786 |
| 12 | 1.9735 | 2.3519 |
| 13 | 2.0276 | 2.3576 |
| 14 | 2.0393 | 2.4245 |

Table 25. Size-specific fecundity of Pine and Archer *S. exspinosus* populations. P > .05 at all sizes.

| Length (mm) | Pine | Archer |
|---|---|---|
| 1.229-1.341 | 4.00 | ----- |
| 1.342-1.454 | 4.17 | 5.00 |
| 1.455-1.568 | 5.65 | 4.75 |
| 1.569-1.681 | 7.45 | 8.60 |
| 1.682-1.795 | 12.13 | 9.60 |
| 1.796-1.908 | 14.69 | 12.55 |
| 1.909-2.021 | 15.85 | 14.42 |
| 2.022-2.135 | 14.60 | 15.16 |
| 2.136-2.248 | 12.00 | 16.35 |
| 2.249-2.362 | 21.00 | 18.08 |
| 2.363-2.375 | 18.00 | 20.60 |
| 2.476-2.588 | 5.00 | 27.00 |

Table 26. Age-specific fecundity of Pine and Archer *S. exspinosus* populations.

| Days | Pine | Archer | p |
|---|---|---|---|
| 3 | 9.00 | 3.00 | <.05 |
| 4 | 7.00 | 9.80 | >.05 |
| 5 | 6.86 | 8.50 | >.05 |
| 6 | 7.63 | 15.82 | <.05 |
| 7 | 11.20 | 15.88 | >.05 |
| 8 | 14.75 | 16.85 | >.05 |
| 9 | 14.50 | 16.50 | >.05 |
| 10 | 15.13 | 13.43 | >.05 |
| 11 | 10.67 | 20.00 | >.05 |
| 12 | 13.71 | 16.09 | >.05 |
| 13 | 13.20 | 17.50 | >.05 |
| 14 | 13.87 | 13.80 | >.05 |

Table 27. A. Mean pigmentation ranks for 3 species of *Simocephalus* from 8 collection sites.
B. Analyses of variance and Kruskal-Wallis k-sample tests of pigmentation rank means.

| A. Species | | Mean | n |
|---|---|---|---|
| *S. exspinosus* | Pine Pond | 4.15 | 40 |
| | Archer | 1.00 | 40 |
| | Mt. Vernon Pond | 1.00 | 40 |
| *S. vetulus* | Pine Pond | 4.03 | 40 |
| | Lake Alice | 2.85 | 40 |
| | Psychology Pond | 1.75 | 50 |
| *S. serrulatus* | River Styx Bridge | 2.97 | 40 |
| | Stock Pond | 1.18 | 40 |

| B. Habitat comparisons | ANOVA p= | Kruskal-Wallis p= |
|---|---|---|
| Archer/Mt. Vernon/ Pine | .0001 | .0001 |
| Stock/River Styx | .0001 | .0001 |
| Alice/Psychology/Pine | .0001 | .0001 |
| Alice/Psychology | .0001 | .0001 |
| Alice/Pine | .0001 | .0001 |

Table 28. Relationship between eyespot size and body length of *S. exspinosus* not exposed to visually-oriented predation (Archer) and exposed to visually oriented predation (Pine, Puddle, and Mt. Vernon Ponds).

| Body length range (mm) | 1.40-1.59 | 1.60-1.79 | 1.80-1.99 | 2.00-2.19 | 2.20-2.39 |
|---|---|---|---|---|---|
| Archer | | | | | |
| Sample size | 14 | 15 | 23 | 30 | 12 |
| $\bar{X}$ body length (mm) | 1.530 | 1.701 | 1.883 | 2.102 | 2.308 |
| s | 0.065 | 0.067 | 0.059 | 0.061 | 0.055 |
| $\bar{X}$ eyespot size (mm) | 0.087 | 0.091 | 0.096 | 0.106 | 0.113 |
| s | 0.007 | 0.008 | 0.009 | 0.006 | 0.007 |
| Pine, Puddle and Mt. Vernon Ponds | | | | | |
| Sample size | 20 | 17 | 20 | 30 | 27 |
| $\bar{X}$ body length (mm) | 1.500 | 1.709 | 1.878 | 2.114 | 2.317 |
| s | 0.068 | 0.052 | 0.060 | 0.062 | 0.056 |
| $\bar{X}$ eyespot size (mm) | 0.081 | 0.086 | 0.092 | 0.100 | 0.110 |
| s | 0.004 | 0.005 | 0.006 | 0.007 | 0.009 |

Table 29. Age-specific size of all species.

| | Means (mm) | | | | | | |
|---|---|---|---|---|---|---|---|
| Day | *S.exs* | *S.vet* | *S.ser* | DF/df | f | p | Duncan |
| 0 | 0.7125 | 0.5882 | 0.6279 | 2/284 | 122.45 | .0001 | *exs ser vet* |
| 1 | 0.9272 | 0.8051 | 0.8358 | 2/244 | 37.11 | .0001 | *exs ser vet* |
| 2 | 1.2671 | 1.0353 | 1.0716 | 2/268 | 63.56 | .0001 | *exs ser vet* |
| 3 | 1.5377 | 1.2304 | 1.3317 | 2/245 | 83.76 | .0001 | *exs ser vet* |
| 4 | 1.7331 | 1.3691 | 1.4840 | 2/268 | 114.24 | .0001 | *exs ser vet* |
| 5 | 1.8314 | 1.4644 | 1.6091 | 2/243 | 84.06 | .0001 | *exs ser vet* |
| 6 | 1.9546 | 1.5502 | 1.7089 | 2/267 | 119.75 | .0001 | *exs ser vet* |
| 7 | 2.0212 | 1.6163 | 1.8450 | 2/242 | 92.82 | .0001 | *exs ser vet* |
| 8 | 2.0975 | 1.6749 | 1.8991 | 2/264 | 117.81 | .0001 | *exs ser vet* |
| 9 | 2.1667 | 1.7222 | 1.9762 | 2/240 | 123.68 | .0001 | *exs ser vet* |
| 10 | 2.2151 | 1.7649 | 2.0000 | 2/251 | 130.68 | .0001 | *exs ser vet* |
| 11 | 2.2495 | 1.7936 | 2.0843 | 2/241 | 136.52 | .0001 | *exs ser vet* |
| 12 | 2.2945 | 1.8155 | 2.0866 | 2/242 | 137.27 | .0001 | *exs ser vet* |
| 13 | 2.3205 | 1.8424 | 2.1599 | 2/230 | 146.74 | .0001 | *exs ser vet* |
| 14 | 2.3538 | 1.8677 | 2.1686 | 2/226 | 132.72 | .0001 | *exs ser vet* |

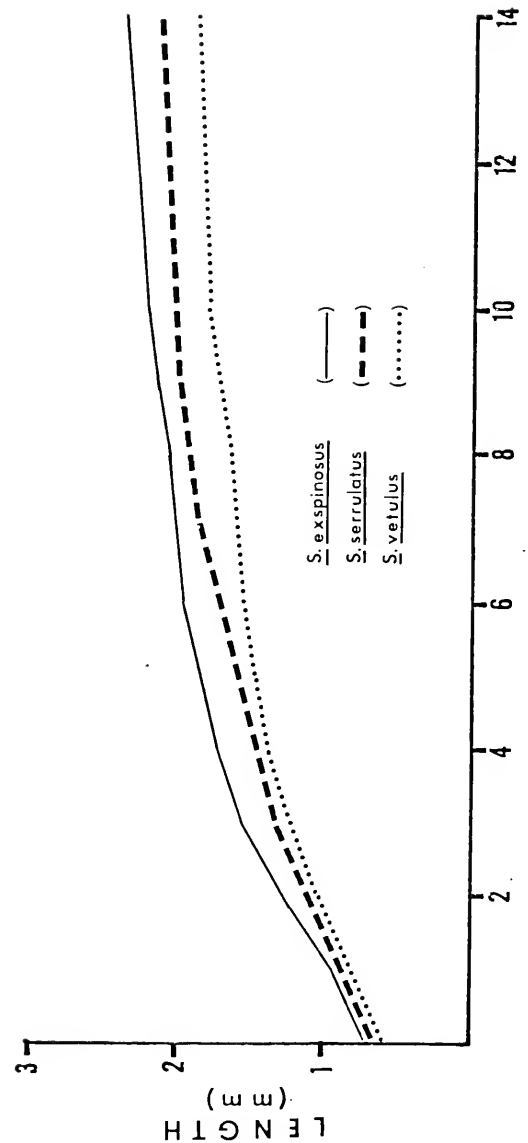


FIGURE 2: Age-specific size for all species.

Table 30. Size-specific fecundity of all species.

| mm | Mean young *S.exs* | *S.vet* | *S.ser* | DF/df | f | p | Duncan |
|---|---|---|---|---|---|---|---|
| 1.134-1.228 | ---- | 4.50 | 3.00 | 1/1 | .12 | .7877 | |
| 1.229-1.341 | 4.00 | 4.11 | 3.00 | 28/2 | .29 | .7508 | |
| 1.342-1.454 | 4.29 | 6.73 | 7.31 | 2/73 | 2.51 | .0880 | |
| 1.455-1.568 | 5.61 | 10.24 | 5.95 | 2/95 | 22.73 | .0001 | *vet ser exs* |
| 1.569-1.681 | 7.25 | 14.77 | 9.37 | 2/135 | 60.17 | .0001 | *vet ser exs* |
| 1.682-1.795 | 10.18 | 17.46 | 13.59 | 2/153 | 35.17 | .0001 | *vet ser exs* |
| 1.796-1.908 | 12.85 | 19.16 | 15.81 | 2/197 | 38.70 | .0001 | *vet ser exs* |
| 1.909-2.021 | 14.75 | 20.81 | 18.28 | 2/113 | 15.46 | .0001 | *vet ser exs* |
| 2.022-2.135 | 15.15 | ---- | 19.76 | 1/115 | 30.12 | .0001 | |
| 2.136-2.248 | 16.85 | ---- | 19.82 | 1/77 | 6.36 | .0137 | |
| 2.249-2.362 | 18.90 | ---- | 23.82 | 1/58 | 11.32 | .0014 | |
| 2.363-2.475 | 20.80 | ---- | 22.00 | 31/1 | .16 | .6919 | |
| 2.476-2.588 | 27.93 | ---- | ---- | 14/0 | | | |
| 2.589-2.702 | 24.13 | ---- | ---- | 7/0 | | | |
| 2.703-2.815 | 28.75 | ---- | ---- | 7/0 | | | |
| 2.816-2.929 | 36.00 | ---- | ---- | 0/0 | | | |
| 2.930-3.042 | 21.50 | ---- | ---- | 0/0 | | | |

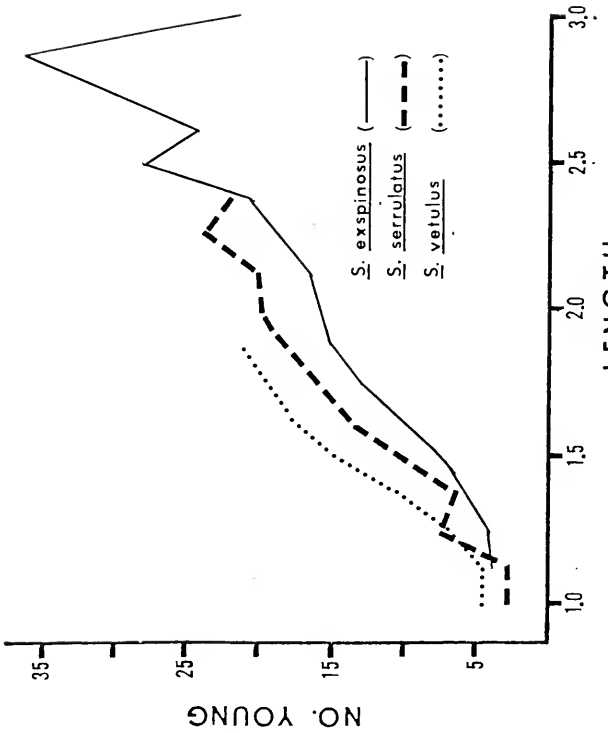


FIGURE 3: Size-specific fecundity for all species.

Table 31. Age-specific fecundity of all species.

| Day | *exsp.* | *vet.* | *ser.* | DF/df | f | p | Duncan |
|---|---|---|---|---|---|---|---|
| 3 | 6.00 | 2.67 | 4.80 | 2/12 | 1.71 | .2221 | |
| 4 | 8.58 | 7.00 | 7.00 | 2/75 | 2.29 | .1086 | |
| 5 | 8.04 | 6.88 | 8.36 | 2/128 | 1.76 | .1758 | |
| 6 | 16.13 | 13.57 | 13.26 | 2/124 | 3.80 | .0244 | *exsp vet ser* |
| 7 | 13.59 | 14.07 | 16.06 | 98/2 | .97 | .3809 | |
| 8 | 17.50 | 16.54 | 18.77 | 2/136 | 1.32 | .2712 | |
| 9 | 16.63 | 17.16 | 19.71 | 2/75 | 1.24 | .2938 | |
| 10 | 18.29 | 17.73 | 18.63 | 123/2 | .17 | .8464 | |
| 11 | 17.20 | 17.83 | 21.20 | 2/72 | 1.74 | .1827 | |
| 12 | 16.91 | 16.02 | 17.90 | 105/2 | .81 | .4497 | |
| 13 | 16.31 | 16.61 | 20.76 | 2/65 | 3.91 | .0250 | *ser vet exsp* |
| 14 | 15.56 | 16.33 | 17.05 | 96/2 | .73 | .4847 | |

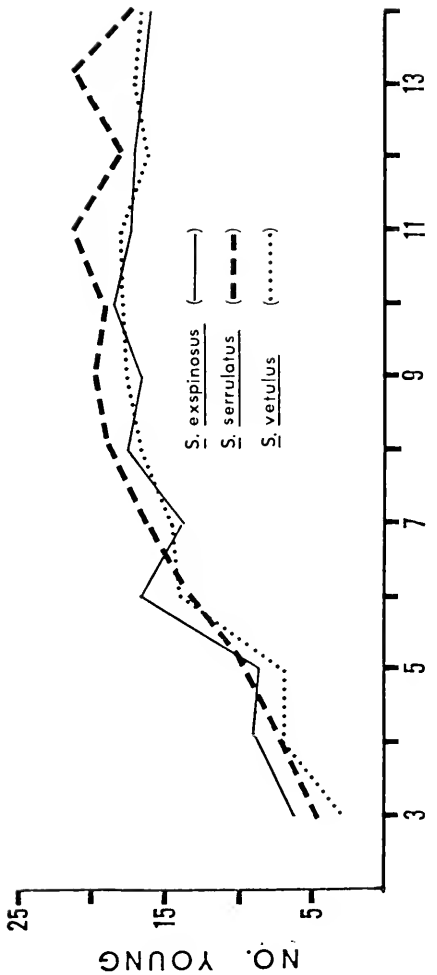


FIGURE 4: Age-specific fecundity for all species.

Table 32. $r_m$ values of all species

| Species | Site | n | $r_m$ | species $r_m$ |
|---|---|---|---|---|
| *S. exspinosus* | Mt.Vernon | 14 | .712 | |
| | Tennis Court | 9 | .685 | |
| | Archer | 18 | .645 | |
| | Santa Fe | 9 | .582 | |
| | Pine | 26 | .566 | |
| | Puddle | 18 | .584 | |
| | | | | .623 |
| *S. vetulus* | Austin Carey | 10 | .691 | |
| | Pine | 13 | .640 | |
| | Lake Alice | 29 | .609 | |
| | Psychology | 26 | .520 | |
| | | | | .615 |
| *S. serrulatus* | River Styx Pond | 17 | .716 | |
| | River Styx Bridge | 19 | .596 | |
| | Stock | 9 | .584 | |
| | | | | .632 |

Analysis of variance: p=.9507

Table 33. Age at first reproduction of all species.

| Species | Mean (days) | n |
|---|---|---|
| *S. exspinosus* | 5.54 | 94 |
| *S. vetulus* | 4.49 | 84 |
| *S. serrulatus* | 4.14 | 49 |

Analysis of variance: p=.0047

Duncan - *exs vet ser*

Table 34. Size at first reproduction of all species.

| Species | Mean (mm) | n |
|---|---|---|
| *S. exspinosus* | 1.6972 | 82 |
| *S. vetulus* | 1.3661 | 83 |
| *S. serrulatus* | 1.4905 | 51 |

Analysis of variance: p=.0001

Duncan - *exs ser vet*

Table 35. Death rates (number of dead/number of days lived) of *Simocephalus* reared to age 14 days.

| Species | Site | Death rate |
|---|---|---|
| *S. exspinosus* | Mt.Vernon | 0.0278 |
| | Archer | 0.0124 |
| | Tennis Court | 0.0336 |
| | Pine | 0.0114 |
| | Puddle | 0.0221 |
| | Santa Fe | 0.0256 |
| *S. serrulatus* | River Styx Bridge | 0.0078 |
| | River Styx Pond | 0.0085 |
| | Stock | 0.0000 |
| *S. vetulus* | Pine | 0.0055 |
| | Psychology | 0.0055 |
| | Lake Alice | 0.0025 |
| | Austin Carey | 0.0146 |

Table 36A. Age-specific size of *S. exspinosus* from 6 sites.

| Day | Mt.Vernon | SantaFe | Archer | TennisC | Puddle | Pine |
|---|---|---|---|---|---|---|
| | | | Mean mm | | | |
| 0 | 0.7605 | 0.7602 | 0.7216 | 0.6970 | 0.6592 | 0.6188 |
| 1 | 1.0070 | 0.9575 | 0.9597 | 0.9575 | 0.8860 | 0.8475 |
| 2 | 1.4096 | 1.2935 | 1.3117 | 1.3986 | 1.1601 | 1.1098 |
| 3 | 1.7414 | 1.6254 | 1.5766 | 1.7010 | 1.4081 | 1.3695 |
| 4 | 1.8722 | 1.9656 | 1.7842 | 1.8760 | 1.5853 | 1.5309 |
| 5 | 2.0953 | 2.0370 | 1.8764 | 2.0200 | 1.6782 | 1.5819 |
| 6 | 2.1656 | 2.2177 | 1.9996 | 2.1043 | 1.8072 | 1.6965 |
| 7 | 2.2710 | 2.2680 | 2.0567 | 2.2763 | 1.9206 | 1.7316 |
| 8 | 2.3950 | 2.3602 | 2.1353 | 2.2586 | 1.9656 | 1.8144 |
| 9 | 2.4271 | 2.4445 | 2.1659 | 2.4109 | 2.0556 | 1.9051 |
| 10 | 2.4812 | 2.4653 | 2.2533 | 2.4109 | 2.0968 | 1.9187 |
| 11 | 2.5092 | 2.5232 | 2.2786 | 2.4528 | 2.1720 | 1.9565 |
| 12 | 2.5625 | 2.5489 | 2.3519 | 2.4714 | 2.1924 | 1.9735 |
| 13 | 2.5734 | 2.6838 | 2.3576 | 2.4948 | 2.2359 | 2.0276 |
| 14 | 2.6384 | 2.6838 | 2.4245 | 2.5175 | 2.2623 | 2.0393 |

Table 36B. Age-specific size of *S. exspinosus* from 6 sites; analysis of variance.

| Day | DF/df | f | p | Duncan |
|---|---|---|---|---|
| 0 | 5/126 | 17.17 | .0001 | MVP SFe Archer TCP Puddle Pine |
| 1 | 5/101 | 5.98 | .0001 | MVP Archer SFe TCP Puddle Pine |
| 2 | 5/110 | 12.30 | .0001 | MVP TCP Archer SFe Puddle Pine |
| 3 | 5/102 | 13.74 | .0001 | MVP TCP SFe Archer Puddle Pine |
| 4 | 5/110 | 23.23 | .0001 | SFe TCP MPV Archer Puddle Pine |
| 5 | 5/100 | 21.12 | .0001 | MVP SFe TCP Archer Puddle Pine |
| 6 | 5/110 | 28.37 | .0001 | SFe MVP TCP Archer Puddle Pine |
| 7 | 5/99 | 25.49 | .0001 | TCP MVP SFe Archer Puddle Pine |
| 8 | 5/106 | 33.36 | .0001 | MVP SFe TCP Archer Puddle Pine |
| 9 | 5/100 | 30.67 | .0001 | SFe MVP TCP Archer Puddle Pine |
| 10 | 5/104 | 32.14 | .0001 | MVP SFe TCP Archer Puddle Pine |
| 11 | 5/94 | 31.22 | .0001 | SFe MVP TCP Archer Puddle Pine |
| 12 | 5/96 | 30.68 | .0001 | MVP SFe TCP Archer Puddle Pine |
| 13 | 5/84 | 28.53 | .0001 | SFe MVP TCP Archer Puddle Pine |
| 14 | 5/86 | 28.52 | .0001 | SFe MVP TCP Archer Puddle Pine |

Table 37A. Age-specific fecundity of *S. exspinosus* from 6 sites.

| Day | Mt. Vernon | S.Fe | Archer | Tennis | Puddle | Pine |
|---|---|---|---|---|---|---|
| 3 | ---- | ---- | 3.00 | ---- | ---- | 9.00 |
| 4 | 9.67 | 3.50 | 9.80 | 12.00 | 6.29 | 7.00 |
| 5 | 9.67 | 8.57 | 8.50 | 12.00 | 8.17 | 6.86 |
| 6 | 20.17 | 21.33 | 15.82 | 18.67 | 16.25 | 7.63 |
| 7 | 20.00 | 17.25 | 15.88 | 24.00 | 11.17 | 11.20 |
| 8 | 26.60 | 22.00 | 16.85 | 20.88 | 14.64 | 14.75 |
| 9 | 26.33 | 21.00 | 16.50 | 20.00 | 13.13 | 14.50 |
| 10 | 20.33 | 26.86 | 13.43 | 25.75 | 17.29 | 15.13 |
| 11 | 29.50 | ---- | 20.00 | 17.00 | 14.17 | 10.67 |
| 12 | 15.00 | 24.20 | 16.09 | 23.83 | 14.38 | 13.71 |
| 13 | 22.00 | ---- | 17.50 | ---- | 16.20 | 13.20 |
| 14 | 18.50 | 18.60 | 13.80 | 19.67 | 15.00 | 13.87 |

Table 37B. Age-specific fecundity of *S. exspinosus* from 6 sites; analysis of variance.

| Day | DF/df | f | p | Duncan |
|---|---|---|---|---|
| 3 | 1/0 | 999 | 0.00 | |
| 4 | 5/30 | 4.33 | .0044 | TCP Archer MV Pine Pu SFe |
| 5 | 42/5 | .83 | .5369 | |
| 6 | 5/40 | 7.36 | .0001 | SFe MV TCP Pu Archer Pine |
| 7 | 5/36 | 3.32 | .0145 | TCP MV SFe Archer Pine Pu |
| 8 | 5/56 | 6.82 | .0001 | MV SFe TCP Archer Pine Pu |
| 9 | 5/18 | 1.80 | .1632 | |
| 10 | 5/49 | 8.02 | .0001 | SFe TCP MV Pu Pine Archer |
| 11 | 4/15 | 4.18 | .0180 | MV Archer TCP Pu Pine |
| 12 | 5/40 | 7.52 | .0001 | SFe TCP Archer MV Pu Pine |
| 13 | 3/12 | 1.14 | .3720 | |
| 14 | 5/37 | 2.60 | .0413 | TCP SFe MV Pu Pine Archer |

Table 38. Size at first reproduction of *S. exspinosus* from 6 sites.

| Site | n | Mean size (mm) |
|---|---|---|
| Santa Fe | 9 | 1.9656 |
| Tennis Court | 8 | 1.9516 |
| Mt. Vernon | 8 | 1.8900 |
| Puddle | 13 | 1.6602 |
| Archer | 18 | 1.6568 |
| Pine | 26 | 1.5135 |
| total | 82 | 1.6972 |

Analysis of variance: p=.0001

Duncan: Santa Fe Tennis Mt. Vernon Puddle Archer Pine

Table 39. Age at first reproduction of *S. exspinosus* from 6 sites.

| Site | n | Mean age (days) |
|---|---|---|
| Santa Fe | 9 | 4.78 |
| Puddle | 18 | 4.75 |
| Pine | 26 | 4.69 |
| Archer | 18 | 4.33 |
| Tennis Court | 9 | 4.33 |
| Mt. Vernon | 14 | 4.21 |
| total | 94 | 4.54 |

Analysis of variance: p=.0236

Duncan: Puddle Santa Fe Pine Archer Tennis Mt.Vernon

Table 40A. Size-specific fecundity of *S. exspinosus* from 6 sites.

| Length (mm) | Arch. | Mt.Ver. | T.C. | S.Fe | Pu. | Pine |
|---|---|---|---|---|---|---|
| 1.229-1.341 | ---- | ---- | ---- | ---- | ---- | 4.00 |
| 1.342-1.454 | 5.00 | ---- | ---- | ---- | ---- | 4.17 |
| 1.455-1.568 | 4.75 | ---- | ---- | ---- | 7.00 | 5.65 |
| 1.569-1.681 | 8.60 | ---- | ---- | ---- | 5.71 | 7.45 |
| 1.682-1.795 | 9.60 | 7.00 | 14.00 | 6.00 | 7.80 | 12.13 |
| 1.796-1.908 | 12.55 | 9.00 | 11.00 | 6.00 | 11.90 | 14.69 |
| 1.909-2.021 | 14.42 | ---- | 13.17 | 7.67 | 15.50 | 15.85 |
| 2.022-2.135 | 15.16 | 17.25 | 12.25 | 13.80 | 15.80 | 14.60 |
| 2.136-2.248 | 16.35 | 17.00 | 20.83 | 14.00 | 17.60 | 12.00 |
| 2.249-2.362 | 18.08 | 21.40 | 20.00 | 18.14 | 15.57 | 21.00 |
| 2.363-2.475 | 20.60 | 18.40 | 22.57 | 24.17 | 18.00 | 18.00 |
| 2.746-2.588 | 27.00 | 29.00 | 31.20 | 29.40 | 26.00 | 5.00 |
| 2.589-2.702 | ---- | 31.00 | 25.33 | 18.33 | ---- | ---- |
| 2.703-2.815 | ---- | 33.75 | 24.50 | 23.00 | ---- | ---- |
| 2.816-2.929 | ---- | ---- | ---- | 36.00 | ---- | ---- |
| 2.930-3.042 | ---- | ---- | ---- | 21.50 | ---- | ---- |

Table 40B. Size-specific fecundity of *S. exspinosus* from 6 sites; analysis of variance.

| mm | DF/df | f | p | Duncan |
|---|---|---|---|---|
| 1.229-1.341 | 0/0 | | | |
| 1.342-1.454 | 5/1 | .34 | .5868 | |
| 1.455-1.568 | 2/20 | 1.13 | .3431 | |
| 1.569-1.681 | 2/29 | 2.21 | .1282 | |
| 1.682-1.795 | 5/33 | 4.20 | .0046 | TC Pine Archer Pu MV SFe |
| 1.796-1.908 | 5/54 | 4.46 | .0019 | Pine Archer Pu TC MV SFe |
| 1.909-2.021 | 4/50 | 3.61 | .0116 | Pine Pu Archer TC SFe |
| 2.022-2.135 | 60/5 | .95 | .4580 | |
| 2.136-2.248 | 5/35 | 1.33 | .2746 | |
| 2.249-2.362 | 5/43 | 1.80 | .1327 | |
| 2.363-2.475 | 5/24 | 1.46 | .2407 | |
| 2.476-2.588 | 5/9 | 3.11 | .0667 | |
| 2.589-2.702 | 2/5 | 3.34 | .1199 | |
| 2.703-2.815 | 2/5 | 1.44 | .3208 | |
| 2.816-2.929 | 0/0 | | | |
| 2.930-3.042 | 0/0 | | | |

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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